

The Atna River: Studies in an Alpine–Boreal Watershed

Developments in Hydrobiology 177

Series editor
K. Martens

The Atna River: Studies in an Alpine–Boreal Watershed

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Reprinted from Hydrobiologia, volume 521 (2004)



Springer Science+Business Media, B.V.

Library of Congress Cataloging-in-Publication Data

A C.I.P. Catalogue record for this book is available from the Library of Congress.

ISBN 978-90-481-6624-4 ISBN 978-1-4020-2254-8 (eBook)

DOI 10.1007/978-1-4020-2254-8

Cover illustration: 'Vinternatt i Rondane' (A winter's night in Rondane) by Harald O. Sohlberg, 1914.
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Originally published by Kluwer Academic Publishers in 2004

Softcover reprint of the hardcover 1st edition 2004

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Preface

The discussion on global climate change and loss of biodiversity has documented the need for long-term series of environmental data. Collection of meteorological data for more than 150 years has been an important basis for the climatic change debate. As for meteorological phenomena, we do know that there are natural long-term fluctuations also for biological species and populations. Long-term series of biological data are, however, almost non-existent. This lack of long-term data series from reference sites, and the complexity of ecological relationships, makes it difficult to differentiate between changes caused by human activities and natural changes in the environment.

Energy production in Norway is almost exclusively based on hydropower. River regulation for production of electricity affects around 2000 rivers and lakes in the country, and in most of the large river systems water is utilized for energy production. During the last 20–30 years there has been an increased focus on the environmental effects of hydropower development. Environmental impact assessment is now a legally required part of the process of river regulation. Hydrophysical, chemical and biological studies are important elements of this assessment process. These studies have contributed significantly to the general knowledge on freshwater ecology in Norway. However, for the most part, the studies have been short-term, restricted to a couple of years before and after the construction of the power plant. The focus has mostly been on specific rivers or watersheds, with little or no coordination with similar projects in other rivers. The studies have almost exclusively focused on manipulated rivers. Consequently these studies have only to a limited extent thrown light on the long-term natural variation, and their contribution to our ability to differentiate between natural and anthropogenic variation in river systems is restricted.

In order to contribute to these aspects of our understanding of ecosystems, the Norwegian Research Board of Science and Technology (NTNF) in 1983 appointed a committee to develop a multi-disciplinary freshwater research programme called: “Research and Reference River Systems” (FORSKREF). The objective of the programme was to obtain basic information of the long-term development of Norwegian river systems, a necessary tool for differentiating the effects of human manipulation from natural changes. The programme was given a long-term perspective of 10–15 years or more, with a focus on environmental effects of river regulation. In the FORSKREF programme proposal, preference was given to basic research projects, but with participation by applied research institutions.

The underlying idea of FORSKREF was to investigate unregulated rivers, called “Reference Rivers”, with minimum human impact, and with a focus on natural processes. The selected reference rivers were to be reference sites for the effects of human encroachment in rivers, in comparison with the “Research Rivers”, i.e. sites for more thorough scientific studies of cause–effect relationships and of the natural changes. The programme was originally planned to include 12 Norwegian river systems, six regulated and six un-regulated, and distributed all over the country.

When the programme plans were implemented in 1985, four rivers were included, but studies at a level indicated in the original plans started only in two unregulated rivers. These were the River Atna, a tributary to the River Glomma in Hedmark county, and the River Gaula in Sør Trøndelag county. The sampling in Gaula was discontinued in 1990. Therefore the River Atna is the only river system where the original ideas of the FORSKREF programme have been followed up. Due to serious budgets restrictions during the 1990s, the reference aspect has been given priority, providing monitoring type data.

The adjusted objective has been to maintain a coordinated and continuous sampling programme, resulting in data series from 17 continuous years on water flow, temperature, transport of suspended material, water chemistry, phytoplankton, zooplankton, macroinvertebrates and fish at different sites of the River Atna and Lake Atnsjøen. During the whole period, standard sampling methods have been used at the same sites and the result is a unique data series on freshwater physiochemistry and biology. Data from the first 13 years are reported in this volume.

Some studies on cause–effect relations have been carried out and are reported here. However, the data from the River Atna and Lake Atnsjøen have an obvious potential for more studies of this kind. In fact, an important result of this type of programme is to provide datasets that may be used in future studies on long-term changes and cause–effect relationships. The value of the time series increases non-linearly with the number of sampling seasons included, and similar data from other river systems will further increase the potential for future studies.

The present data set from Atna may also be used to improve the design of environmental monitoring programmes in general. Based on this unique data series we are able to analyse aspects such as sampling frequencies, number of sampling sites, and relevance of different parameters and taxa. These are important issues when planning to maximize the cost-benefit aspect of monitoring programmes.

The EU Water Framework Directive will be implemented in Europe and Norway during the coming 10–15 years. Reference conditions are a key concept in the directive and reference values for specific biological elements define the environmental objectives for the different types of water bodies in Europe. Data from this study in Atna will be of great value as reference data for important types of Norwegian waterbodies. When a national biodiversity monitoring programme is established in Norway, the biological monitoring in Atna will be an important part and will give a flying start to the programme by providing historical data.

The data presented in this volume represent more than a decade of freshwater ecology and biodiversity in one specific unregulated watershed, which is nearly untouched by man. Hopefully the unique data series from Atna will demonstrate the great value of this type of long-term coordinated sampling from different disciplines of freshwater science.

STEINAR SANDØY
Directorate for Nature Management
Trondheim, August 2003



Figure 1. A view over Lake Atnsjøen towards the northwest, with Rondane Mountains in the background. Photo: Normanns Kunstforlag.

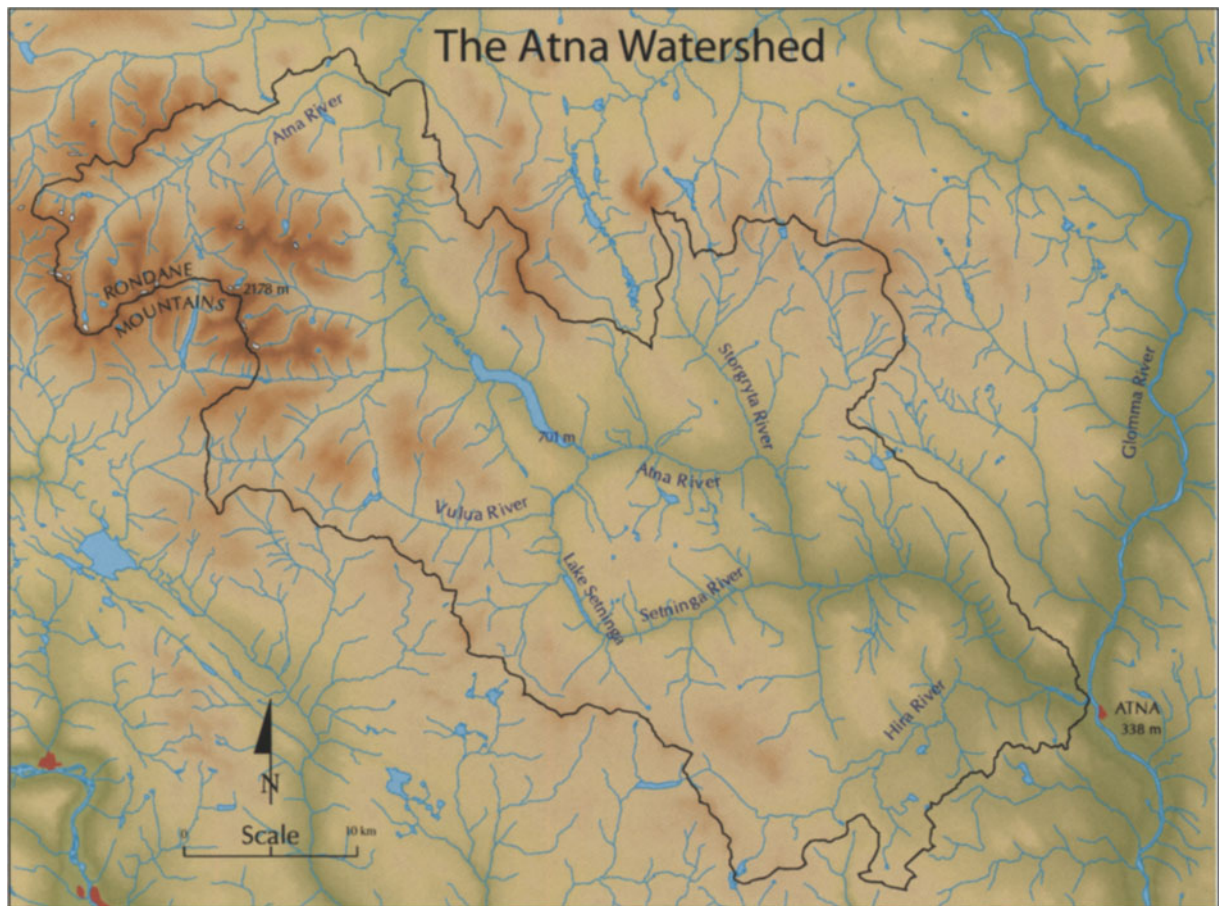


Figure 2. Overview of the Atna watershed. Based on a map from the Norwegian Water Resources and Energy Directorate (NVE).

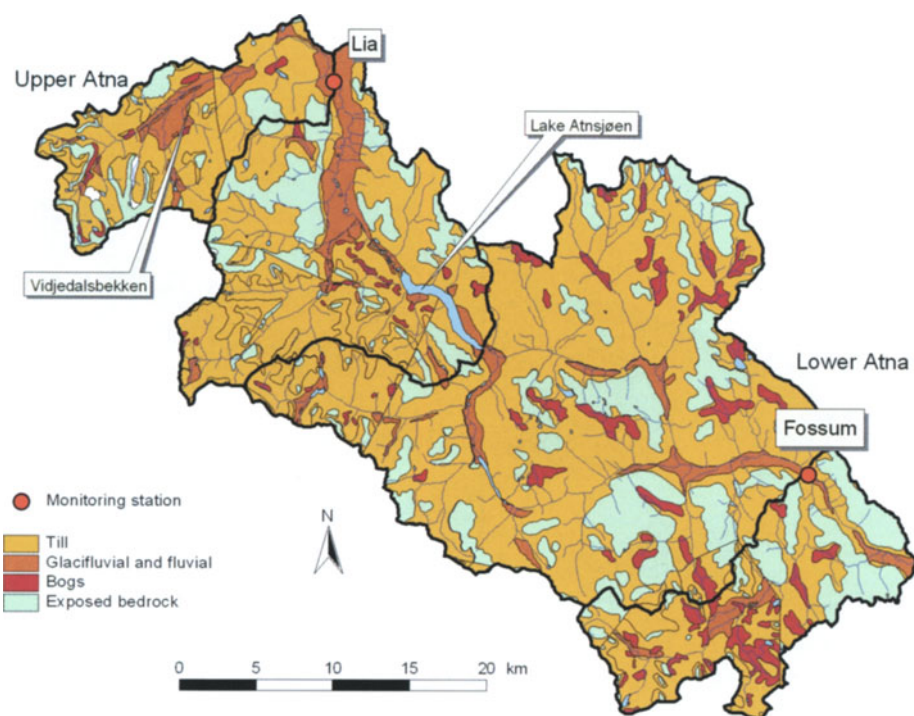


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Figure 6. Snow distribution in the Rondane Mountains after a winter with much snow. Photo taken 12 April, 1988. Photo: Arve M. Tvede.



Figure 7. Snow distribution in the Rondane Mountains after a winter with little snow. Photo taken 15 April, 1996. Photo: Arve M. Tvede.



Figure 8. Several of the source streams of Atna originates in so called 'botn' lakes among the peaks of Rondane Mountain. The botn lake on the picture is at 1466 m a.s.l., adjacent to the mountain Rondvasshøgda. August 2000. Photo: Arve M. Tvede.



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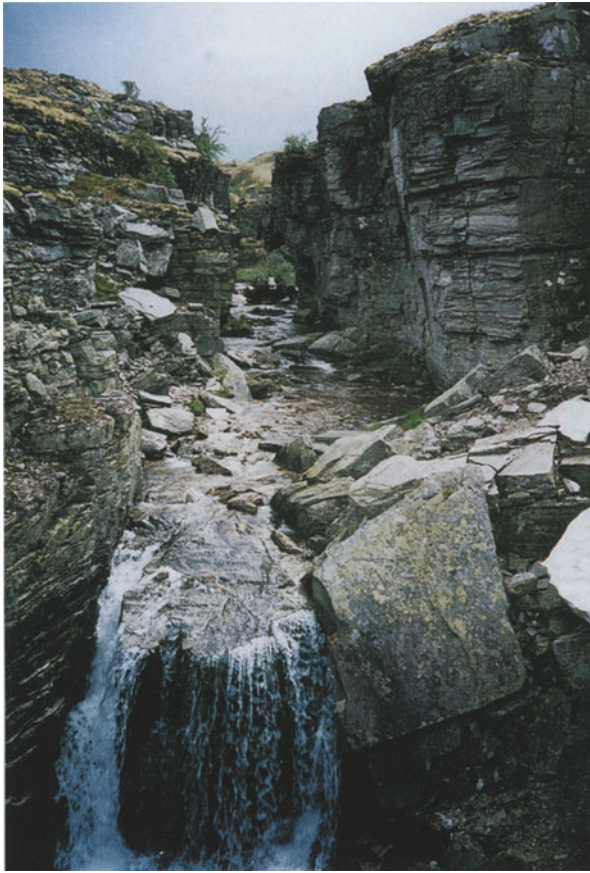


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Figure 15. Occasionally brown trout (*Salmo trutta*) in Lake Atnasjøen may become piscivorous, and reach a good size. But they are far between, and the fishermen often have the outline of their catch carved in wood, to document their good luck. Photo: Trygve Hesthagen.



Figure 16. River Atna passes waterfalls at the outlet of Lake Atnsjøen (at Atnbrua, 701 m a.s.l.). Photo: Trygve Hesthagen.



Figure 17. Atna River looking downstream at Fossum, approximately 420 m a.s.l. May 2003. Photo: Odd Terje Sandlund.



Figure 18. The confluence of Atna with Glomma River, seen from the eastern bank of Glomma, 338 m a.s.l. May 2003. Photo: Odd Terje Sandlund.



Figure 19. The Lia Bridge hydrological station, 758 m a.s.l., in the upper part of the Atna River. Photo: Arve M. Tvede.



Figure 20. Ice conditions in Atna River at Gammelgarden, approximately 710 m a.s.l., 16 April, 1996. The ice is formed by a static process and has a smooth surface. Photo: Arve M. Tvede.



Figure 21. Ice conditions in Atna River at Fossum, 420 m a.s.l., 23 April, 1987. The ice has been formed by a dynamic process from drifting frazil and has an uneven surface. Photo: Arve M. Tvede.



Figure 22. Ice conditions in the tributary Storbekken, 780 m a.s.l., 15 April, 1996. Following an unusually cold winter the ice has filled up the whole stream bed. Photo: Arve M. Tvede.

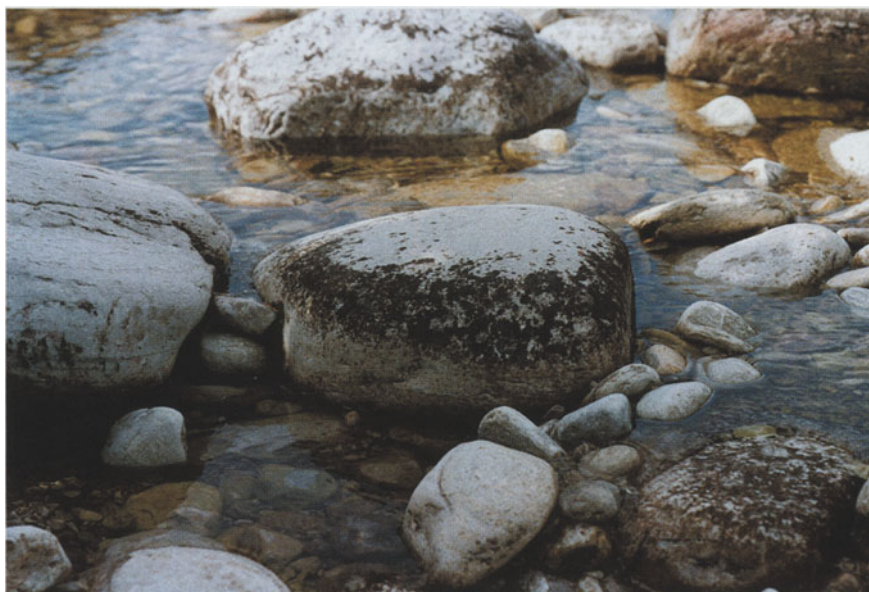


Figure 23. At Dørålen, 1020 m a.s.l., in June 1992, there is little algal growth except a dark brown crust of the cyanobacterium *Scytonematopsis starmachii*. Photo: Eli-Anne Lindstrøm.



Figure 24. Luxuriant growth of the bryophyte *Fontinalis squamosa* at Elgvassli, 740 m a.s.l., September 2001. Also shown is the sampling frame for recording benthic vegetation. Photo: Stein W. Johansen.



Figure 25. Bright green tufts of the green alga *Oedogonium* c (24–29 my) on the bryophyte *Fontinalis dalecarlica* in the permanently submerged zone at the outlet of Lake Atnasjøen, October 2001. Photo: Stein W. Johansen.



Figure 26. In some years the cyanobacterium *Phormidium autumnale* develops a dark patchy cover directly on stones in late autumn. From the tributary River Setninga, October 2001. Photo: Stein W. Johansen.



Introduction to the Atna research area

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Background

In the 1960s, the Atna watercourse was subject to various plans for major hydropower development. The plans were met with strong public opposition right from the beginning due to the anticipated environmental damage in an area with a wide array of natural values. As a result, the Norwegian Parliament in 1973 decreed a 10-year protection period for the Atna watercourse to allow a proper assessment of the environmental aspects. The findings formed the basis for the 1985 decision to permanently protect the Atna watercourse from hydropower development. This decision, and the extensive collection of scientific baseline data in a wide range of environmental studies, led to the selection of the Atna watershed as a national research and reference catchment. The FORSKREF program ('Research in reference watercourses') was established in October 1984.

The drainage area

The Atna river basin is located in the northeastern part of south Norway, in Hedmark and Oppland counties. The river system drains a catchment area of 1318 km² which extends from the highest summits of over 2000 m a.s.l. in the Rondane mountains in the west down to the confluence with River Glomma at 338 m a.s.l. (NOU, 1983). This confluence is also River Atna's most easterly point (Fig. 1). The hypsometric curve for the basin, which has a mean

altitude of 1020 m a.s.l., shows that only 10% of the area is below 720 or above 1400 m a.s.l. (Fig. 2). There are presently no glaciers in the Rondane mountains, but a few permanent snowfields persist in some of the highest cirques. Approximately 50% of the Atna watershed is situated above the upper tree-line (1000–1150 m a.s.l.).

River Atna originates in a small tarn 1446 m a.s.l. at the head of the cirque named Verkisdalsbotn, in the far west of the catchment area. For the first 25 km the river heads northeast through Døråldalen mountain valley, descending below the tree line into the sub-alpine birch forest after 12–13 km, at about 1100 m a.s.l. At Dørålseter Tourist Lodge the river is joined by Vidjedalsbekken tributary from the south. At 750 m a.s.l., the river turns abruptly towards the southeast and with steadily decreasing gradient reaches Lake Atnsjøen at 701 m a.s.l. The main river is joined by several tributaries along this stretch. The largest is the river Store Myldinga from the west. Between Gammelgarden and Lake Atnsjøen, River Atna has a well developed meandering channel.

Lake Atnsjøen is the largest lake in the water course with a surface area of 4.8 km². It is a typical fjord lake (formed in a glacial valley) with steep sides and a relatively flat bottom. The lake basin is 8.9 km long and varies between 0.5 and 0.8 km in width (cf. Fig. 1 in Halvorsen, 2004). Maximum depth is 80 m, mean depth is 35 m, and the theoretical retention time has been calculated at 6 months.

Just below the outlet of Lake Atnsjøen, River Atna forms a significant waterfall. Below this waterfall, the river flows in a series of rapids and pools towards Storbekkmoen where it is joined by the tributary Setninga from the west. River Setninga drains the sub-

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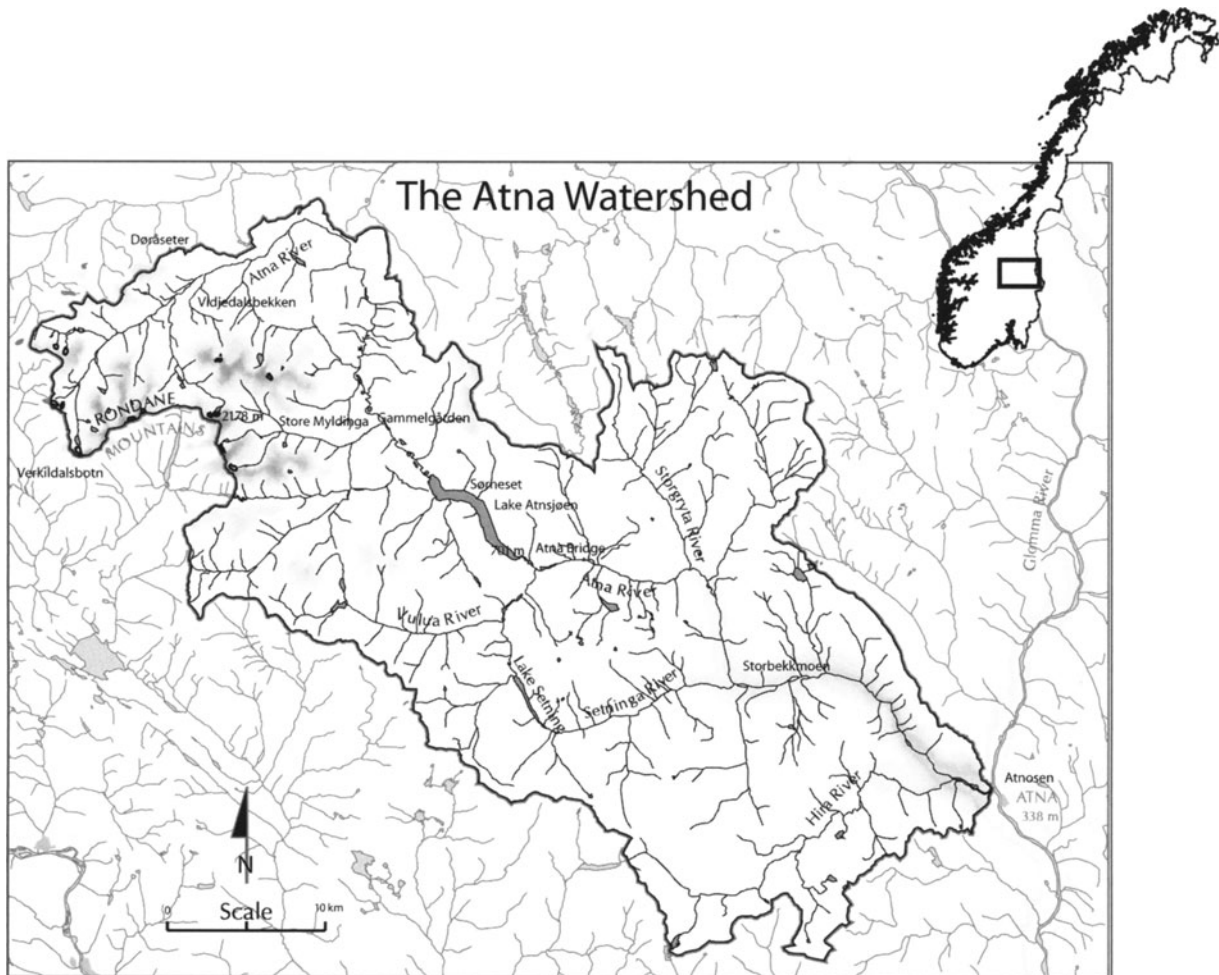


Figure 1. The Atna river basin. Based on a map from the Norwegian Water Resources and Energy Directorate (NVE).

alpine and boreal forest areas southeast of Rondane. This tributary includes one sizeable lake, called Setningen (altitude 757 m; surface area 0.7 km²). Below the River Setninga confluence, River Atna continues towards the southeast with an even gradient until it finally meets River Glomma at the small Atnosen settlement. Just before Atnosen, River Atna is joined by a relatively large tributary from the southwest, River Hira. River Atna's total length from Verkisdalsbotn to Atnosen is 97 km with a descent of about 1100 m.

A large part of the Rondane National Park lies within the Atna watershed. Rondane is Norway's oldest national park and was established by Parliament in 1962. The main reasons for the establishment of the national park were the impressive mountain landscape, the large population of wild reindeer (*Rangifer tarandus*), and the virtually pristine alpine and

subalpine ecosystems including the upper reaches of River Atna. There are plans to enlarge the park by also including the subalpine forest areas to the west of Lake Atnsjøen. The large wetlands north of the lake, Atnasjømyrene, are protected as a nature reserve, mainly due to its rich bird life.

The climate in the Atndalen valley is continental, with cold winters and relatively warm summers (Nordli & Grimenes, 2004). Annual precipitation may be as low as 400 mm in the lower parts, but increases considerably with altitude, and is more than 1000 mm in the Rondane mountains.

The vegetation

The vegetation and plant diversity of the Atna watershed is quite well documented (Dahl, 1956; Moss &

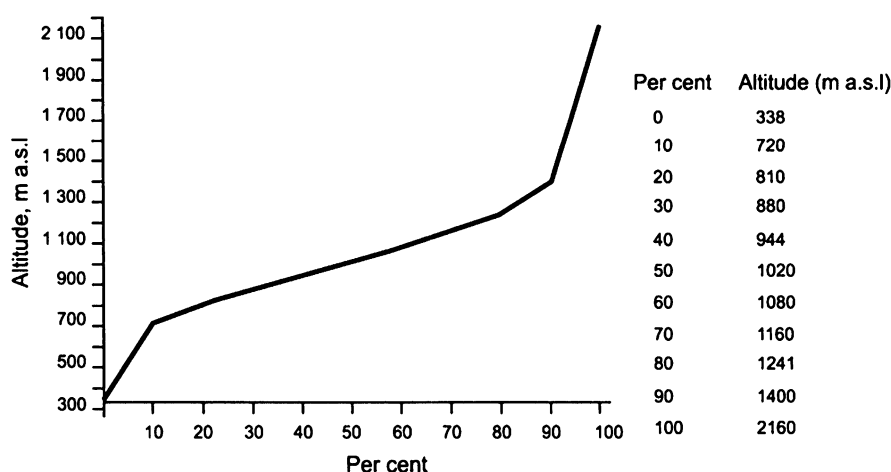


Figure 2. Hypsometric curve for the Atna river basin. Calculated in ARC/INFO based on the Norwegian Mapping Authority's map series N250.

Skattum, 1986). A summary of the botanical data is given by Andersen (1986).

Vegetation zones ranging from middle boreal in the lower parts of the watershed to high alpine in the Rondane mountains are represented. The tree-line is situated between 1000 and 1150 m a.s.l. Only some smaller areas on the highest mountain peaks belong to the high alpine zone, while 40–45% of the watershed belongs to the low and middle alpine zone. Boreal and subalpine vegetation dominates the lower areas.

In the area north and northwest of Lake Atnsjøen the nutrient-poor sparagmite, the well-drained moraine and glacialfluvial material combine with low precipitation to produce extremely species poor vegetation types. Lichen- and heath-dominated vegetation types with low productivity cover large areas. A very distinctive characteristic of the subalpine and alpine part of the watershed is the large continuous areas covered by reindeer lichens (especially *Cladonia stellaris*). This vegetation type is probably better developed in this area than in any other part of southern Norway.

In the subalpine zone, the lichen and heath vegetation constitutes the lower layers in open forests of pine (*Pinus sylvestris*) and birch (*Betula vulgaris*), and in the low alpine zone together with only birch. More frost- and wind-resistant vegetation mostly consisting of reindeer lichens and grasses (Graminidae) cover the barren snow-free ridges. Snow beds are found in the more sheltered depressions, with vegetation dominated by blueberry (*Vaccinium myrtillus*), thickets of juniper (*Juniperus communis*) and dwarf birch (*Betula nana*), or heaths dominated by grasses and sedges.

Real snow bed vegetation, dominated by liverworts and dwarf willows (*Salix* spp.), is found only occasionally. Only in very small areas, along the rivers and tributaries, and in depressions with more permanent moisture, is there more luxuriant vegetation. This may consist of meadows dominated by tall herbs.

The Atnsjømyrene wetland area covers large areas in the Atna valley north of Lake Atnsjøen. These large marshland complexes consist of ombrotrophic and poor minerotrophic bogs, small lakes, sedge marshes, willow thickets and flooded alder woods. Large areas are flooded almost every year during the snow melt floods in spring.

Due to richer bedrock and soils, the nutritional conditions are generally much better in the south-eastern part of the watershed, especially in the sub-catchments of the rivers Setninga and Hira. A considerable number of rich and very rich vegetation types as tall herb vegetation are represented, but mostly in smaller patches. Some patches are especially rich in orchids. However, large areas are dominated by poor vegetation types.

Lichen and heath dominated pine and spruce (*Picea abies*) forest dominates the lower part of the watershed. In areas with better and more stable soil humidity, the dominant vegetation type is blueberry spruce forest, locally with some richer types.

The flora of vascular plants is relatively species rich, as a total of 424 species have been recorded. Most of the species are restricted to the rich vegetation types in sub-catchments of the rivers Setninga and Hira. The area north of Lake Atnsjøen is especially species poor,

with approximately 150 species. The overall flora has a strong continental character.

Human activities

Interventions of a technical nature in the watercourse are very minor, essentially limited to areas below the tree limit. Flood protection work has been carried out on a number of vulnerable reaches both above and below Atnsjøen. Following the extreme flood of 1995, new flood prevention dykes have been built, locally altering the character of the river channel. Presently there is no regulation of the water discharge. When the river was used for timber transport below Lake Atnsjøen, the flow was controlled during early summer by means of a needle dam at the lake outlet. The first sawmill on the river was already in operation at this location by the end of the eighteenth century. Its capacity was increased up to the late 1940s, but the operation closed down about 1960. A small farm hydropower station was built at this waterfall in the mid 1940s. The history of the uses of the river at Atna Bridge have been documented (Brænd, 1994), and are displayed in Atnbrufossen Vannbruksmuseum ('Water Use Museum').

Human settlement along the river consists of scattered farms and areas with other agriculture-related activity. There are some holiday houses and cabins in nearshore areas by Lake Atnsjøen, but otherwise most holiday houses and permanent habitation is located at some distance from the water bodies. One type of intervention with an impact on the watershed and potential indirect effects on the water course are forest clearcutting and the construction of lumber roads, activities which have been increasing over the last 20 years.

Earlier research activities

As documented by Andersen (1986) in a summary of earlier research, the Atna watershed has been subject to scientific research for a long time. In the natural sciences, e.g. geomorphology, botany and zoology, there are a number of classic papers based on data from the area, including research on fish populations in Lake Atnsjøen (Ofte Dahl, 1950; Barth & Hagen, 1951; Dahl, 1956; Gjessing, 1960, 1966).

An important reason for the scientific interest in the Atna area is undoubtedly the research station at Sørnesset, owned by The Norwegian Academy of Science and Letters (Det Norske Vitenskapsakademi). The property was donated to the Academy in 1930

and is situated on the northern shore of Lake Atnsjøen with a magnificent view across the lake towards the Rondane mountains.

Sørnesset has provided a field base for numerous scientists, and it has been a popular venue for informal academic discussions across traditional disciplinary boundaries. Researchers working on the FORSKREF programme have also been able to use the facilities at Sørnesset with permission from the Academy.

The Atna river basin contains exceptionally well preserved deposits and landforms from the deglaciation period and is eminently qualified to be a type area for the valley and the mountain tract of the north-eastern parts of Southern Norway. The River Atna floodplain and delta at the head of Lake Atnsjøen have particularly distinct morphologies. This part of the area is not only a valuable natural archive; it also vividly illustrates present day processes.

The deposits occupying the valley floor in the upper parts of Atna Valley are in places extremely vulnerable and the river channel, the floodplain and the delta would have been destroyed if the hydropower development plans had been implemented. The Atna watershed constitutes a necessary supplement to the landscape inside the Rondane National Park, including natural zonation from the alpine to low boreal zones.

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THE ATNA WATERSHED



The climate of Atndalen

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Key words: temperature, precipitation, climatological periods, climate trends, climate extremes

Abstract

The climate of Atndalen Valley is described by data collected by the standard network of stations currently run by the Norwegian Meteorological institute. It consists of one weather station (Sørneset) with full instrumental equipment, and three precipitation stations with a reduced set of equipment. At the latter stations, precipitation, snow depth, and snow cover are observed. Most of the stations, including the weather station, are situated in the central part of the watershed, near Atnsjøen. The climate of the Atndalen is of a continental type with precipitation minimum in late winter or spring and maximum during summer. The mean annual precipitation is about 500 mm near Atnsjøen (701 m a.s.l.) for the 30 year normal period 1961–1990. At the meteorological station Sørneset the warmest month is July, 11.2 °C, while the coldest month is January, –9.9 °C, i.e. an annual amplitude of 21.1 °C. The mean cloud cover varies from 4.5 oktas in February to 5.4 oktas in July, September and October. The highest ratio of relative sunshine is about 50% in spring. The mean snow depth increases during winter and early spring and reaches its maximum of 68 cm in March. The snow cover disappears on 9 May \pm 12 days and establishes on 5 November \pm 18 days. Variations in precipitation (since 1904) and temperature (since 1864) were studied on a decadal time scale by Gaussian filtering technique, and the significance of trends on the 0.05 level were studied by the Mann–Kendall test. For the whole period no significant trend in annual precipitation was detected. The maximum value was located to the 1920s and the minimum value to the 1910s. Annual mean temperature has increased significantly since 1864, and the classical temperature optimum in the 1930s was surpassed in the 1990s. By adopting a sinus model including the first Fourier component, trends and variations in climatological periods as well as heat and frost sums were studied. The frost free period has since 1864 increased by 13 days within 100 years based on a linear trend line. Earlier passing dates in spring largely account for the increase. The length of the growth season also increased up to about 1950. The annual heat sum shows a linear increase of about 103 daydegrees per 100 years while the annual frost sum varies considerably from period to period and fitted badly with a linear model.

Introduction

The valley of Atndalen is the catchment of River Atna, a tributary to River Glomma (Fig. 1). The altitude of the catchment area varies from 370 m a.s.l. at the confluence with River Glomma to more than 2000 m a.s.l. at the highest peaks in the Rondane Mountains. The large span in altitude leads to a diversity of climates in the Atndalen region. However, the main subject for this analysis will be the valley sections where meteor-

ological data are recorded, i.e. in the central and lower parts of the valley. Largely the analysis is concentrated on precipitation and temperature.

Realising that biological processes as well as various kinds of human activity do not necessarily depend on mean values, climate analysis should also include frequency distributions and probability estimates of rare events. Under the influence of a changing climate, trends and variability of precipitation, temperature and growth season should also be studied. This is by no

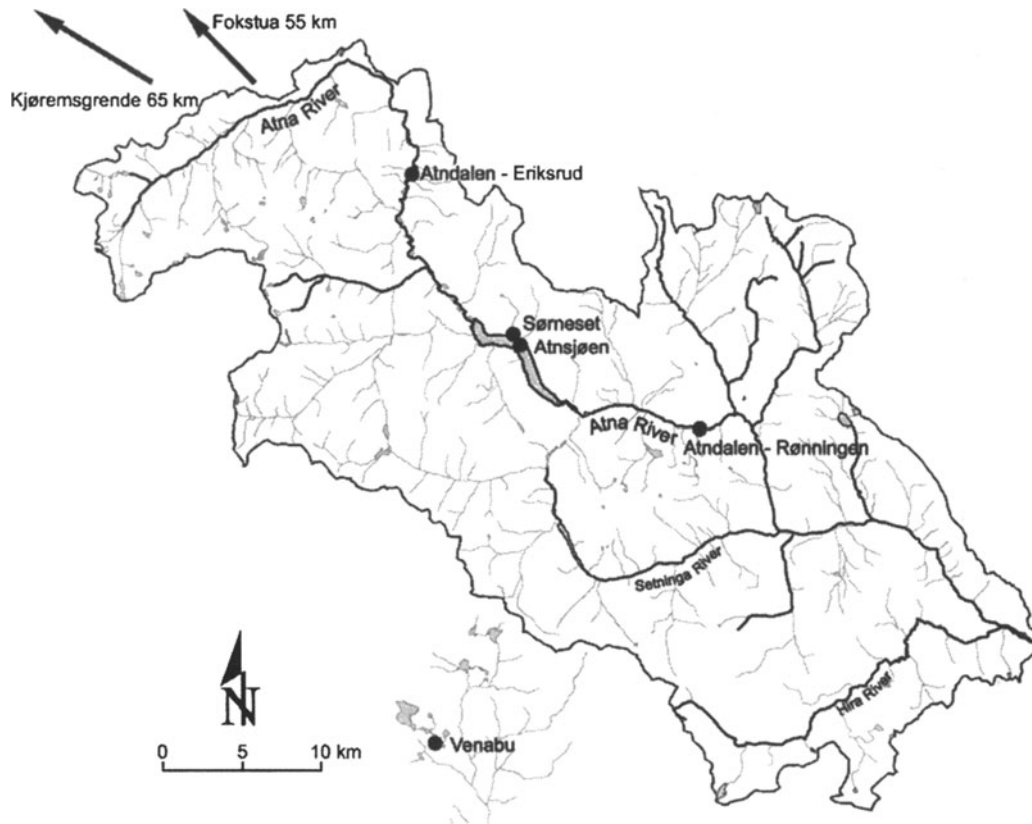


Figure 1. Map of the Atna watershed and surrounding area, with the position of the weather stations listed in Table 1. Arrows indicate direction and distance from Atnsjøen to stations outside the watershed.

means a simple task, because the weather elements, e.g., temperature and precipitation, rarely follow well known distributions. An additional difficulty is the nature of our observations. We have to make our observations at fixed points, while the main course of interest may be the whole area. Therefore it is of paramount importance to apply knowledge of the local climate when interpreting the point observations.

Data

In Atndalen, there is only one weather station, 08710 Sørneset, with a standard observational program. This station was established in 1954 and was meant to be a so called 'secular station', intended for the study of long term trends in climate. The idea was to keep the station's environment constant in order to secure data homogeneity. It has turned out to be a difficult task to maintain the quality of the station, and in recent years there have also been some gaps in the data series. The gaps are interpolated by the use of neighbouring stations on a monthly basis. On a daily base, only short

gaps up to a few days are interpolated while longer gaps are stored in the data base as missing values.

In addition to Sørneset three stations with a reduced observational program are in operation. These are named 'precipitation stations', but snow cover and snow depth are also observed. The stations are listed in Table 1 and their locations are shown in Figure 1. Some stations outside the project area are important sources for climate analyses and are for this reason included in the station list.

The stations are situated from about zero (Eriksrud) up to 50 m (Atnsjøen) above the valley floor. The weather station with full observational program, Sørneset, lies about 40 m above the valley floor.

Climate during the standard normal period, 1961–1990

The valley of Atndalen is well protected in the sector from south-west to north by the central South-Norwegian mountain ridge. Parts of the ridge consist of the Jotunheimen and Dovre mountains. In addi-

Table 1. Meteorological stations currently in operation within the Atna watershed and three additional stations in adjacent areas (*). Category (Cat.): W = Weather station with full observational program, P = Precipitation station.

Station no.	Station name	Start (Year,mm)	Altitude (m)	Latitude	Longitude	Cat.
08450	Atndalen-Rønningen	1971.05	535	61°47' N	10°30' E	P
08710	Sørneset	1954.01	739	61°53' N	10°09' E	W
08720	Atnsjøen	1904.01	749	61°53' N	10°08' E	P
08770	Atndalen-Eriksrud	1971.06	731	61°58' N	10°02' E	P
13420*	Venabu	1980.08	930	61°39' N	10°07' E	W
16610*	Fokstua II	1968.06	972	62°07' N	09°17' E	W
16740*	Kjøremsgrende	1864.06	625	62°06' N	09°03' E	W

Table 2. Monthly and annual precipitation standard normals (mm) 1961–1990 at the four meteorological stations within the Atna watershed.

	Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Des	Year
Atndalen-Rønningen	27	18	19	20	37	62	71	65	51	50	35	30	485
Sørneset	30	22	24	25	40	66	85	71	60	55	43	34	555
Atnsjøen	29	21	23	22	39	62	78	67	57	55	40	31	524
Atndalen-Eriksrud	23	18	19	19	38	64	79	66	60	49	32	23	490

tion, the Rondane Mountains are bordering parts of the valley to the west (Fig. 1). This causes little precipitation to fall under wind in the protected sector from south-west to north. However, deep depressions in connection with warm fronts may pass through or redevelop on the eastern side of the mountains. Cold air advection does not result in precipitation in winter, but in summer some afternoon showers may be the result.

In the remaining sector local mountains are too low to effectively reduce precipitation. On a regional scale the terrain is rising from east to west and this may enhance the amount of precipitation coming from the east. On the eastern slopes of Rondane Mountains, i.e. the western side of the upper Atndalen, the effect might be quite substantial.

Normals in meteorology are standardised to distinct periods, mainly to facilitate easy comparison of data. The currently used period, 1961–1990, is therefore adopted in the present paper. However, for the ongoing investigations in Atndalen, the applied reference period is 1986–1998. As climate undergoes decadal variations, mean values for the two periods are not expected to be equal. In order to facilitate easy comparison to other papers in this volume, val-

ues for the 1986–1998 reference period is given in Appendix I.

Climate near the valley floor

Winds from south-west and west are by far the most common wind directions over Norway at the altitudes where precipitation is released. This leaves Atndalen in the rain shadow most of the time. The annual precipitation amounts only to about 500 mm at the measuring stations in the normal period 1961–1990 (Table 2). Precipitation is at its minimum (about 20 mm per month) in late winter and early spring, but increases in late spring and early summer, reaching its maximum level in July (around 80 mm). This differs from other areas in south-eastern Norway where maximum precipitation occurs in the autumn, and from some coastal districts of Western Norway where the maximum is in winter. In the continental climate of Atndalen, the mid-summer maximum is ascribed to a high frequency of showers.

The monthly standard normals of mean temperature (1961–1990) at the measuring site Sørneset (739 m a.s.l.) are shown in Table 3. The warmest month is July (11.2 °C) and the coldest month is January (−9.9 °C), i.e. an annual amplitude of 21.1 °C on a monthly basis.

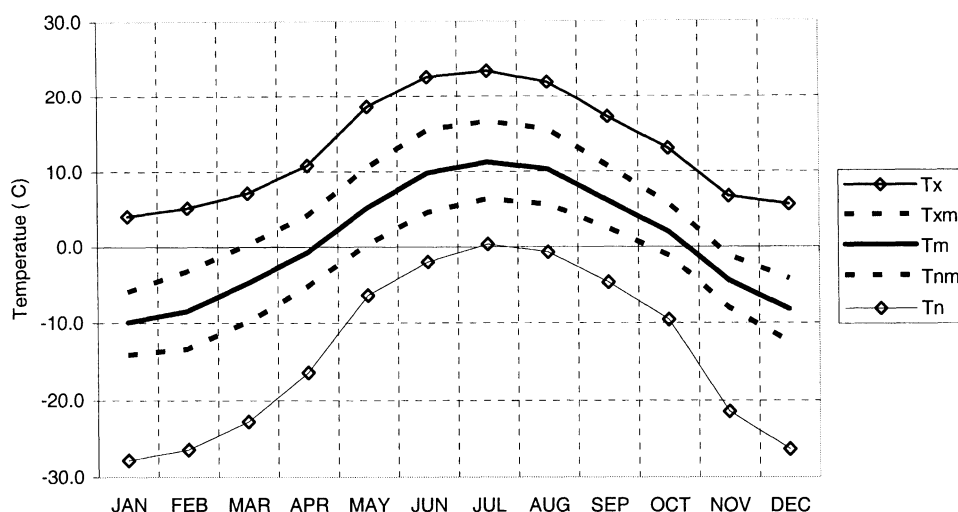


Figure 2. Monthly standard normals (1961–1990) of mean temperature (Tm), daily maximum temperature (Txm), daily minimum temperature (Tnm), monthly maximum temperature (Tx) and monthly minimum temperature (Tn), at the weather station Sørneset.

Table 3. Monthly and annual air temperature standard normals ($^{\circ}\text{C}$) 1961–1990 at the weather station Sørneset, and at five stations (*) in the vicinity of the Atna watershed.

	Altitude m a.s.l.	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Des	Year
Alvdal*	485	-11.4	-9.7	-4.3	0.6	6.6	11.3	12.5	11.4	6.9	2.3	-4.8	-9.5	1.0
Kjøremsgrende*	626	-8.7	-7.6	-3.9	0.2	6.5	10.7	12.0	11.1	6.6	2.4	-3.9	-7.2	1.5
Sørneset	739	-9.9	-8.4	-4.8	-0.7	5.2	9.8	11.2	10.3	6.1	2.0	-4.5	-8.2	0.7
Venabu*	940	-9.7	-9.2	-6.6	-2.3	4.2	9.2	10.4	9.3	4.6	0.3	-4.5	-8.1	-0.3
Fokstua I*	952	-10.3	-9.5	-7.0	-2.9	3.8	8.4	10.0	8.9	4.4	0.4	-5.7	-8.6	-0.7
Fokstua II*	974	-8.8	-8.2	-6.0	-2.4	4.0	8.5	9.8	9.0	4.6	0.9	-4.7	-7.3	0.0

During the year the first month with above zero mean temperature is May, and the last month is October (Fig. 2).

From March to October the mean daily maximum (Txm) is above zero with a maximum in July of 16.7°C . The mean daily minimum temperatures (Tnm) also reaches its maximum of 6.4°C in July, while its minimum is reached in January with -14.1°C (Fig. 2).

The difference between Txm and Tnm is called the Daily Temperature Range (DTR). As shown in Figure 2, DTR remains approximately constant, about 10°C , most of the year, but in the autumn it is considerably smaller, 6.9°C and 6.8°C , in October and November, respectively. One important reason for the small DTR during autumn is the fact that Atnsjøen acts to reduce the temperature decrease during night by releasing heat stored in the water during summer.

The monthly means of the absolute maximum (Tx) and minimum temperatures (Tn) in the normal period 1961–1990, show that the maximum Tx is 23.5°C in July, which is also the only month with Tn above zero, 0.3°C (Fig. 2). In the coldest month, January, Tn is as low as -27.8°C .

Cloud cover prevents direct sunshine from heating the ground and if the cloud cover persists during night, it also reduces net radiation loss. Thus, the amount of clouds in the sky to a large extent affects the radiation balance and thereby also daily temperature range (DTR). Except in the coldest season, a large cloud cover is associated with a small DTR, and vice versa. At Sørneset the mean amount of cloud varies within one okta only (Table 4). The minimum value (4.5 oktas) occurs in February, and the maximum in July, September and October (5.4 oktas).

Sørneset is one of the few meteorological stations in Norway where the duration of bright sunshine is

Table 4. Standard monthly normals, 1961–1990, for the weather station Sørneset: Hours of bright sunshine duration; Relative sunshine duration (%); Mean cloud cover (oktas), Mean snow depth (cm).

Weather element	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Des
Sunshine	20.4	72.0	127.7	169.7	204.1	196.6	181.7	168.0	120.0	80.9	33.1	9.4
Rel. sunshine	17.7	35.9	41.3	44.5	46.9	43.0	40.4	41.0	35.1	31.9	21.5	12.9
Cloud cover	4.6	4.5	4.8	4.8	4.9	5.1	5.4	5.3	5.4	5.4	5.1	4.7
Snow depth	47	60	67	58	12	0	0	0	0	2	16	32

measured (Table 4). The maximum length of the day occurs in June, but the maximum hours of bright sunshine occurs in May due to less cloud cover.

Sunshine duration is obviously dependant on the length of the day, particularly at high latitudes. The term relative sunshine duration, i.e. sunshine duration relative to the time the sun is over the horizon, aims to level out this dependency. In spring, relative sunshine duration is almost 50%, while in December it is below 13% (Table 4).

The mean monthly snow depth increases during winter and reaches its maximum value, 67 cm, in March. It remains high (58 cm) also in April, but decreases abruptly from April to May. The mean date of snow disappearance in spring (and the establishment of snow cover in autumn/winter) is studied by analysing the snow cover data from the whole series of digitised data (database: Atnsjøen 1957–1998). The timing of snow cover disappearance (or establishment) is defined as the last day in spring (or the first day in autumn/winter) when 25% or less (or more) of the ground was snow covered.

During the 42 years of data, the snow cover disappeared 9 May ± 12 days, while permanent snow cover was established 5 November ± 18 days. The day of disappearance was nearly normally distributed, but the day of snow cover establishment was skewed with a long tail towards winter. In fact the latest establishment of snow cover was 3 January while the earliest was 13 October. The earliest and latest days of snow disappearance were 11 April and 30 May, respectively.

Spatial variation in precipitation and temperature

Climate parameters are known from point measurements, and it is often difficult to know how well the weather stations represent the general area. It will certainly vary from one weather element to another. In the Atna catchment area there is only one meteorological station recording several weather elements. While there are several stations measuring precipita-

tion, they are all situated within an elevation above the valley floor of 50 m.

The annual precipitation varies slightly along the valley (Table 2), and there appears to be a local maximum at Atnsjøen (555 mm, station Sørneset). The systematic differences seem to occur due to precipitation during winter. The reduced precipitation downstream of Atnsjøen may be caused by the commonly observed increase in precipitation with height (Førland, 1979), while reduced precipitation upstream from Atnsjøen may be due to favourable sheltering conditions. There are discharge measurements at the outlet of Atnsjøen corresponding to about 680 mm yr⁻¹ of precipitation. If we assume an evaporation loss of about 300 mm yr⁻¹, mean precipitation in the catchment area upstream of Atnsjøen amounts to about 1000 mm yr⁻¹. With an observed precipitation of approx. 500 mm yr⁻¹ at the observation station, this means that in the high altitude parts of the catchment area, where there are no weather stations, precipitation must exceed 1000 mm yr⁻¹.

In the mean troposphere temperature decreases with height, but near the ground, especially at high latitudes, the situation is far more complex. Based on Norwegian data, Bruun (1955) found that the gradient of mean monthly temperature vs. altitude varied between about -0.7°C per 100 m in summer and about -0.5°C per 100 m in mid winter for 'well ventilated stations'. Tveito (1998), using regression analysis, found values between -0.3°C and -0.7°C , i.e. results very similar to those of Bruun.

In order to extrapolate mean temperature based on data from Sørneset, 739 m a.s.l., gradients of -0.7°C per 100 m seems reasonable for the period June–October. With a July normal at Sørneset of 11.2°C , the normal 10°C July isotherm would be situated at about 910 m a.s.l. In May, when the snow cover disappears at Sørneset, but still is intact at higher altitudes, the gradient may be even steeper. The difference between the two stations Kjøremsgrende and Fokstua II, which

are close to the Atna watershed (cf. Table 3), is for example in April and May -0.75°C per 100 m. At fair weather conditions in winter a layer of cold air is often generated near the ground leading to an inverse temperature gradient, i.e. the temperature is increasing with height above the ground. In particular these inversions are common in December and January and might in the long run outweigh the situations with decreasing lapse rate. In winter, mean temperatures at Sørneset might therefore be representative also for somewhat higher altitudes, as is the case for the Kjøremsgrenda station.

When ice cover is established on Atnsjøen, normally in mid November (Tvede, 2003), the mean vertical gradient changes abruptly. A valley/lake landscape similar to Atndalen/Atnsjøen was studied by Nordli (1990). His results transferred to the Atndalen means that the vertical gradient would change from autumn values (approx. -0.7°) to winter values (approx. 0.0°) as soon as the ice cover is established on Atnsjøen. Upstream from the lake, the gradients would change less abruptly. This applies also to the northern lake shore where cold air often is draining southward (cf. Nordli, 1999).

At Atnsjøen the valley is U-shaped with the lake covering almost the whole flat area at the valley floor. From the outlet of the lake to Storbekkmoen, about 20 km downstream, the valley is more narrow and V-shaped. In this section the valley floor becomes steeper, in particular in the lowest 5 km. Altitude decreases from 700 m at the outlet to 500 m at Storbekkmoen. Given a winter inversion situation with ice-cover on Atnsjøen, cold air normally drains down along the valley. Under the force of gravity and due to the narrowing of the valley, the speed of the drainage flow increases. Cold air is mixed with some warmer air from higher altitudes and temperature at low altitudes increases (Gotaas & Nordli, 1985). Thus, the temperature during winter in the lower part of the valley from Atnbrua to Storbekkmoen is assumed to be higher than at Atnsjøen. Upstream of Atnsjøen, the valley floor has a low gradient for the first 10–15 km and the temperature near the valley floor is expected to be quite uniform.

The normals for extreme temperatures shown in Figure 2 are not representative for higher altitudes than the measuring site. At the time of the day when temperature reaches its maximum, the inversions are absent, except in mid winter. Thus, the gradients for the mean daily maximum temperature (T_{xm}), and the mean monthly maximum temperature (T_x) are

expected to be slightly steeper than for mean temperature. However, the gradient must be less steep than -1°C per 100 m, the dry adiabatic temperature gradient. At the time of the day when temperature reaches its minimum, inversions predominate most of the year. At the valley side, gradients of both mean daily minimum temperature (T_{nm}) and mean monthly minimum temperature (T_n) are expected to be positive. The magnitudes are very difficult to estimate and especially the T_n will vary with the topography on a small scale. During the period from about mid-summer to the time when the ice cover is established on Atnsjøen, inversions are generally absent over the lake.

As T_{xm} decreases and T_{nm} increases with altitude, it is evident that the daily temperature range, DTR, decreases with altitude.

Long term variations and trends of precipitation and temperature

Precipitation

The oldest precipitation station still in operation in Atndalen is 08720 Atnsjøen. It has full data coverage since 1904. Gaussian low pass filtering technique was used on the data series in order to study the variations of annual and seasonal precipitation sums. Variations on a decadal time scale were studied by choosing a standard deviation of 3 years in the Gaussian distribution. The results are shown in Figure 3. Visually some of the curves indicate that there are trends in the precipitation data since 1904. The significance of these trends was determined by the non-parametric Mann–Kendall significance test (Sneyers 1990) used on the unfiltered values.

The curve in Figure 3 representing the annual sum of precipitation rises abruptly in the early 1920s and levels out just before 1930. Another local maximum is in the late 1980s. Local minima are present in the 1910s and 1970s. Both the increased precipitation up to 1930 and the decrease from the 1980s are significant at the 0.05 level. For the whole period there is no significant trend in precipitation.

Variation in seasonal precipitation is shown in Figure 4. The pattern of local maxima and minima seems to be quite different between the seasons. For example, in the autumn a local maximum occurred in the 1980s while in the same decade a minimum occurred in winter. As already mentioned, summer contributes more than the other seasons to the annual precipitation sum, and the pattern of the annual precipitation can be

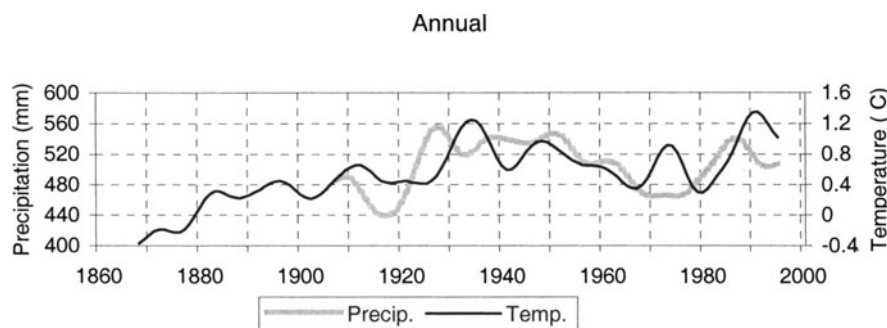


Figure 3. Mean annual temperature for weather station Sørneset for the period 1865–1998 and annual precipitation sums for Atnsjøen for 1904–1998. For methods, see text.

traced back to the summer curve, with especially high values in the four decades between 1920 and 1960. In summer the increase from the start of the series is significant up to the four rainy decades, but it is not significant for the whole series.

Analysing the whole data series shows no significant trends in spring and summer. In the winter and autumn seasons, however, significant trends at the 0.05 level were detected, negative in winter and positive in autumn. This means that there has been a reduction in winter precipitation and an increase in autumn precipitation.

Temperature

The Sørneset temperature series dates back to 1954. To facilitate a study of the temperature climate on a longer time interval, the series was generated back to 1864 by ‘simple linear regression analysis’ with the Kjøremsgrende series as predictor. Regression lines for each month were calculated during the common overlapping period 1954–1998. The regression coefficients varied from 0.99 in January, February and March to 0.94 in May. Composite annual and seasonal time series 1864–1998 valid for Sørneset were established, prior to 1954 by the regressions, and from 1954 on the basis of observations. The same Gaussian filter as for precipitation (see above), was also used for the study of decadal temperature variations. The Mann–Kendall test was used for testing the significance of trends.

The annual means show a significant positive trend during the whole series from 1865 to 1998. The filtered curve passes 0°C around 1880 and remains above zero. The trend is significant also for the first years of the curve. By adding one by one year to the series and performing successively testing, the significance of the trend can be examined in detail. It

reaches the 0.05 significance level in 1910. From the 1920s, the temperature continues to increase; quite abruptly up to the 1930s where a local maximum is located. This maximum was not surpassed before warm years in the 1990s were included in the series.

Since the 1930s the variability on a decadal scale has increased compared with the oldest part of the curve. The local maxima are situated around 1950 and in the 1970s, while the local minima are found in the early 1940s, in the 1960s, and around 1980.

The seasonal curves (Fig. 4) show that some of the local extremes occur in the same decades in three or even four of the seasons. This applies to the warm spells in the 1930s and 1970s and the cold spells in the 1900s and 1960s. The summer maximum in the 1930s and the autumn maximum around 1960 have still not been exceeded, while in spring and winter the maxima are located in the 1990s.

During the whole period 1865–1998, significant positive trends at the 0.05 level were detected in spring and autumn, while no trends were detected in winter and summer. Since the 1980s, trends were detected in winter and autumn, with winter temperatures increasing, and autumn temperatures decreasing.

In mild winters precipitation tends to be larger than in cold winters. The main factor is that dry continental air masses predominate during cold winters. Though significant at the 0.01 level, correlation between precipitation and temperature is, however, rather poor ($r = 0.28$). During the other seasons, there is no significant correlation between precipitation and temperature.

Global mean temperature has increased significantly since the 1860s when the network of weather stations had increased sufficiently to enable calculation of reliable global means. But during this period, the temperature has periodically been stable and even

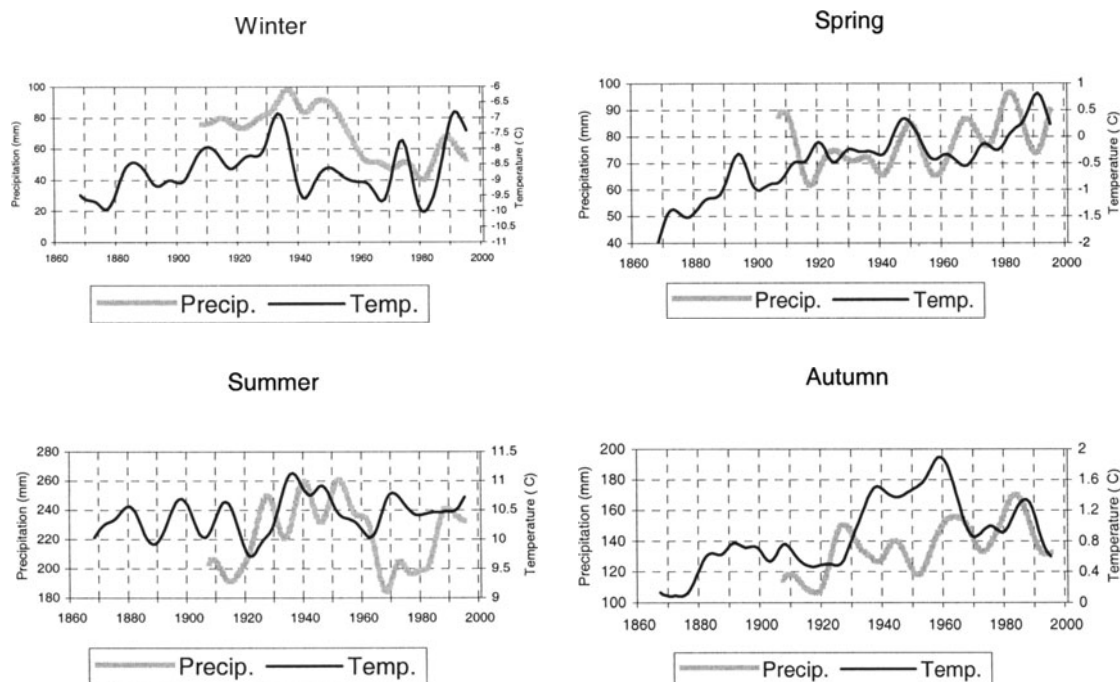


Figure 4. Mean seasonal temperatures for weather station Sørneset (1865–1998) and seasonal precipitation sums for Atnsjøen (1904–1998). The seasons are: Winter (Dec.–Feb.), Spring (Mar.–May), Summer (Jun.–Aug.), Autumn (Sep.–Nov.). For methods, see text.

decreased. Such a period occurred globally from the 1940s to about 1980. After 1980 the earlier mean values have been surpassed (Houghton et al., 1996). In Southern Norway, the early maximum occurred already in the 1930s, and the historical maximum was not exceeded until the 1990s (Hanssen-Bauer & Nordli, 1998).

In Atndalen, the combined effect of the mild winters in the 1990s and increasing temperatures in spring have contributed to the historical annual temperature maximum of the 1930s being exceeded. The autumn maximum in the 1930s has also been exceeded in the 1990s, but still the warmest decadal summer temperatures were recorded in the 1930s.

Duration of climatological periods, heat and frost sums

In the temperate zone, the daily mean temperature varies through the year approximately as a sinus function (Grimenes & Nissen, 2004). Based on monthly mean temperatures at the station Sørneset for periods of 15 years, a sinus model including the first order Fourier series component gave a good correlation to the observed values, with R^2 -values between 0.993 and 0.999. This model was used as a tool for the regeneration of smoothed daily mean temperatures for each

period. As the model evens out the variation from year to year in the 15-year period, variables of interest for the period may be calculated by the means of simple function analysis. For Sørneset the temperature data are divided into nine 15-year periods, starting in 1865 (except the 14-year period from 1985 to 1998). Model outputs discussed here are annual mean temperature, the length of the frost free period, the length of the growth season, the heat sum and the frost sum.

The average length of the frost free part of the year in each 15-year period is shown in Figure 5. The tendency is that the date when the average daily temperature passes the freezing point in spring appears earlier in recent periods. For the corresponding date in the autumn, the tendency is not as clear and less linear. The number of days between these two dates, i.e. the average length of the frost free period, shows a clear tendency. If linear regression is applied, the increase in the length of the frost free period is 13 days per 100 years. It is also seen from the figure that the frost free part of the year is longer in the four latter 15 year periods than in the five earlier periods.

The length of the growth season is defined as the number of days with temperatures $\geq 5^\circ\text{C}$. Figure 6 shows that the length of the growth season increased

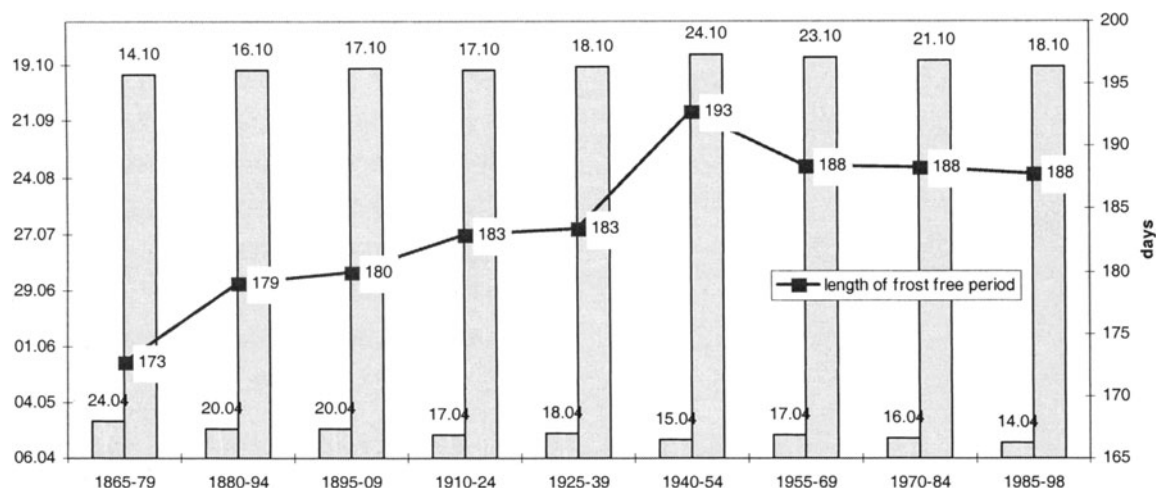


Figure 5. Length of the frost free period in number of days (right axis; ■—■) corresponding to each 15-year period from 1865 to 1998 at weather station Sørneset. Also shown are the dates (left axis, columns) when the daily mean temperature passes the freezing point (0 °C) in the spring and in the autumn, respectively.

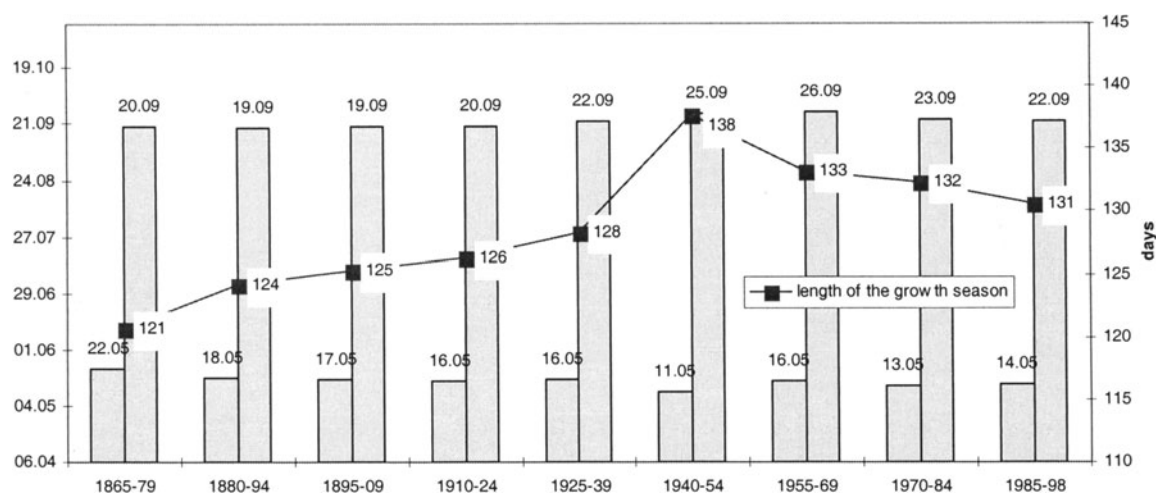


Figure 6. Length of the growth season in number of days (right; ■—■) corresponding to each 15-year period from 1865 to 1998 at weather station Sørneset. Also shown are the dates (left axis, columns) when the daily mean temperature passes 5 °C in the spring and in the autumn respectively.

steadily from 1865–79 to 1940–54, but that it has declined slightly since then.

Annual heat sum is the sum of each daily mean temperature of 5 °C or more. (e.g.: The heat sum for three days with mean temperature 4.2 °C, 5.4 °C and 7.5 °C respectively, equals 2.9 day-degrees). The variable is frequently used in agro-sciences describing the climatic conditions for crops. Annual frost sum is the equivalent variable, summing up each daily mean temperature below 0 °C. The unit for both variables is 'day-degrees'.

Annual heat sum and annual frost sum for Sørneset is shown in Figure 7. Annual heat sum shows a linear tendency. When linear regression is applied, we find an increase of 103 day-degrees per 100 years. The annual frost sum can hardly be adapted to a linear function.

Annual mean temperatures for the 15-year periods are shown in Figure 8. There is apparently a high negative correlation ($R = -0.95$, $P < 0.05$) between annual mean temperature and frost sum.

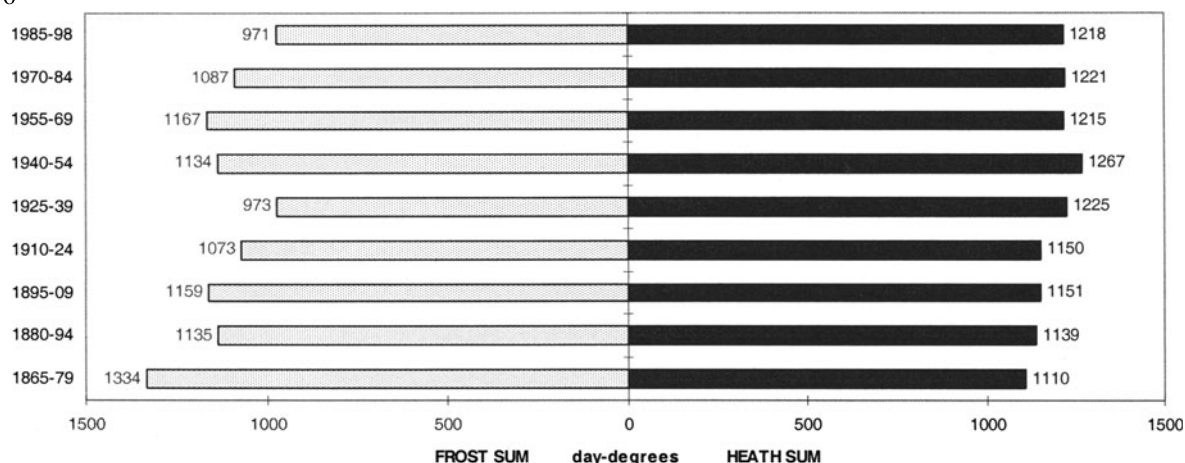


Figure 7. Mean annual heat sum and mean annual frost sum for the 9 15-year periods from 1865 to 1998 at weather station Sørneset.

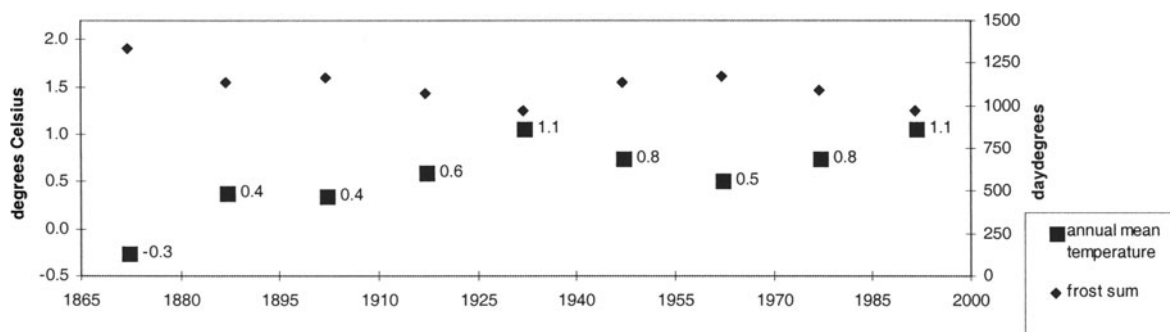


Figure 8. Mean annual temperature for 15-year periods from 1865 to 1998 for weather station Sørneset. Frost sums are also shown. Note the negative correlation between mean annual temperature and frost sum.

In Appendix II some model calculations are given for the common reference period, 1986–1998, and the standard normal period 1961–1990.

Frequency distribution of daily temperature and precipitation

Mean values only leave us with an incomplete knowledge of climate. Unusual temperatures and precipitation are also important for biological processes. For example, temperatures below certain limits may kill eggs of certain pest insects, preventing potential damage of birch trees (Tennow & Holmgren, 1987). In order to indicate the frequency distributions of daily precipitation sums, as well as daily maximum and minimum temperatures, the 5, 25, 50, 75 and 95 percentiles have been calculated (Table 5). In order to obtain the best possible estimates for the tails of the distributions, it is preferable to use data for a maximum length of the observation periods. In reality, 1957 is the earliest available year because of the lack

of older digitised daily values. There are also some gaps in the series from Sørneset, but no attempts have been made to fill the gaps except for the routine data control. The total length of the data series is thus reduced to about 40 years. For precipitation, however, complete data coverage 1957–1998 (42 years) is obtained by replacing Sørneset by the neighbouring station Atnsjøen.

The temperature in winter has fallen below -40°C three times (two episodes) during the 40 years of observation, the coldest being -42.0°C recorded 31 December 1978. At this time a cold spell struck south-eastern Norway. However, the temperature distribution curve has a long negative tail and already the 5 percentile is substantially higher, i.e. -27.2°C or about 15°C higher than the absolute minimum.

Frost has occurred in summer at about 5% of the days and on 6 June 1971 the lowest minimum temperature was recorded, -5.0°C . In summer, minimum temperature is nearly normally distributed and the

Table 5. Percentiles of precipitation sums (mm, normal period 1961–1990) for the precipitation station Atnsjøen and daily maximum and minimum temperatures for the weather station Sørneset. Days without measurable precipitation are excluded (61% in winter, 63% in spring, 52% in summer, and 57% in autumn).

	Min	5%	25%	Median	75%	95%	Max.
Winter:							
Precipitation		0.1	0.4	1.2	3.1	7.8	21.0
Maximum temperature	−34.5	−16.0	−8.0	−4.0	0.0	5.0	13.0
Minimum temperature	−42.0	−27.2	−19.0	−12.3	−6.9	−1.8	7.6
Spring:							
Precipitation		0.1	0.3	1.0	3.1	9.5	30.6
Maximum temperature	−12.5	−3.7	1.0	4.9	8.9	15.9	22.7
Minimum temperature	−33.3	−19.0	−8.5	−3.5	0.0	4.0	10.0
Summer:							
Precipitation		0.1	0.9	2.9	6.8	15.8	61.2
Maximum temperature	5.0	10.0	13.0	15.5	19.0	23.3	28.5
Minimum temperature	−5.0	0.0	3.5	5.9	8.1	10.9	17.6
Autumn:							
Precipitation		0.1	0.5	2.0	5.2	13.3	40.0
Maximum temperature	−22.5	−6.0	1.0	5.8	10.0	15.0	24.0
Minimum temperature	−30.1	−15.0	−5.2	−1.0	2.4	6.6	12.5

standard deviation is lower than in the other seasons, i.e. 3.3 °C in summer compared to 6.8 °C in spring. The difference between the 25 and 5 percentiles are 3.5 °C in summer compared to 10.5 °C in spring.

The extreme maximum temperature 28.5 °C, has in fact been observed twice, on 2 August 1982 and 19 June 1970. Also in spring and autumn temperatures above 20 °C are occasionally observed. Maximum temperature is nearly normally distributed in winter, spring and autumn, but not in summer, when the distribution curve has a long tail on the positive side.

The variable ‘days of precipitation’ requires some explanation. Precipitation is quite often observed in so small amounts that nothing is seen in the gauge, i.e. the precipitation is unmeasurable. The observers are instructed to write 0.0 mm for the precipitation amount and add a proper precipitation symbol. However, so small amounts of precipitation may easily be overlooked and during night this certainly happens. To avoid the problem, a precipitous day is in this article defined as a day with measurable precipitation.

The precipitation distribution curve is far from normal. In Atndalen it is more common not to have than to have precipitation within one day, see the figures of non-precipitous days for each season in the heading of Table 5. To give room for the precipitation distribution

curve, all non-precipitous days were excluded from the data before the calculation of the percentiles was performed.

As expected, the summer season with the largest precipitation sum also had the largest values of one day precipitation (Tables 2 and 5). Altogether five events in summer exceeded the largest one day precipitation at other seasons (40 mm); the highest one, 61.2 mm, was measured 4 July 1982. This is more than 10% of the annual precipitation sum. Winter and spring are the driest seasons. Their seasonal sums are nearly equal but their distributions differ. The maximum value are higher, the 75 percentile value is equal, while the 25 and 50 percentile values are lower in spring than in winter. This means that in precipitous weather situations, there is in spring a higher probability for large precipitation events than in winter although the seasonal sums are nearly equal. In autumn and summer, however, all percentiles are higher than in winter and spring.

Extreme precipitation events often lead to flooding, and have therefore received special focus by meteorologists and community alike. At The Norwegian Meteorological Institute (met.no), the method currently in use for estimating the recurrence periods for one day precipitation events is a modified version of

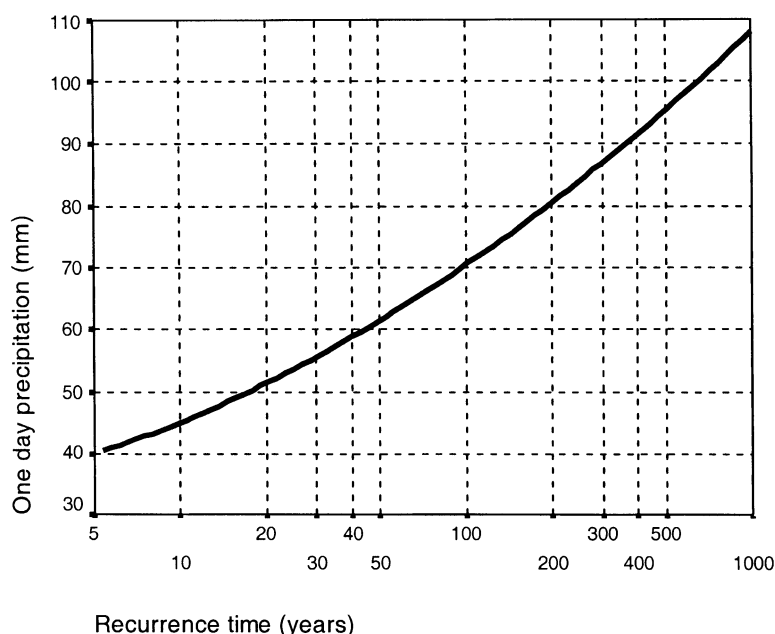


Figure 9. Recurrence periods for one day precipitation at weather station Atnsjøen based on the data period 1954–1998. For methods, see text.

the method originally developed by the Environmental Research Council (NERC), in the UK (Førland, 1992).

Met.no's method was applied on the Atnsjøen annual series of one day precipitation, i.e. the same data as used in the percentile calculations. The largest observed one day precipitation of 62 mm was found to have a recurrence period of 50 years, while one day precipitation of 40 mm has a recurrence period of only 5 years, see Figure 9. One day precipitation of 70 mm was estimated to have a recurrence period of 100 years.

This method allows for estimating recurrence times of up to 1000 years. However, estimating the recurrence time for very rare events involves large uncertainties. On one occasion in 1997, Fulufjället Mountain, which is about 150 km east of Atndalen, received about 400 mm rain within 24 hours (Alexandersson et al., 1997). It may be interesting to consider if something similar could occur also in the Atna watershed. The station Atnsjøen is situated in a valley while Fulufjället is a hill or mountain. Therefore, the orographic mechanisms for precipitation enhancement may be quite different at the two sites. However, this incidence at Fulufjället far exceeded what had been estimated as a probable event by the Swedish Meteorological and Hydrological Institute. Could this rare weather situation, giving the huge amount of rainfall, in some fundamental way be different from more

moderate heavy rainfall situations? If so, the estimated probability of very unusual precipitation events is likely to be too low. These considerations may not be valid the Atnsjøen locality, but they indicate that the right end of the curve in Figure 9 (reflecting the longest recurrence periods) should be used with great caution.

In this volume a severe flooding situation is described by Tvede (2004) in the first days of June 1995. This situation, however, was not like the situation at Fulufjället. At Atndalen the highest one-day precipitation was only about 25 mm, which by no means is an unusual amount of precipitation during one day in summer, see Figure 9. However, 25 mm was observed at two consecutive days. In the days before, rainy weather had saturated the soil as well as the remaining snow cover. Thus, the natural reservoirs were full, which contributed strongly to the severity of the flooding.

Conclusions

The climate of Atndalen is of a continental type with precipitation minimum in late winter or spring (about 20 mm per month) and maximum during summer (about 80 mm per month). The annual precipitation amounts to about 500 mm. These figures apply to the central part of the watershed, i.e. the areas around Atnsjøen (701 m a.s.l.) during the normal

period 1961–1990. However, in high altitude areas of the watershed, annual precipitation probably exceeds 1000 mm. The maximum one day precipitation observed at Atnsjøen is 62 mm, which is estimated to have a recurrence period of about 50 years.

At the meteorological station Sørneset near Atnsjøen, the warmest month is July (11.2 °C) while the coldest month is January (−9.9 °C), i.e. the annual temperature amplitude is 21.1 °C. In July, the mean daily maximum and the mean monthly maximum temperatures are 16.7 °C and 25.5 °C, respectively. In January, the mean daily minimum and mean monthly minimum temperatures were −14.1 °C and −27.8 °C, respectively. In winter (December–February), the 5 percentile of daily minimum temperature is −27.2 °C while in summer (June–August), the 5 percentile of the daily maximum temperature is 23.3 °C.

In the normal period the mean cloud cover varies from 4.5 oktas in February to 5.4 oktas in July, September and October. The highest ratio of relative sunshine is about 50% in spring. The mean snow depth increases during winter and early spring and reaches its maximum, 67 cm, in March. The snow cover disappears on 9 May \pm 12 days and establishes on 5 November \pm 18 days.

Variations in precipitation (since 1904) and temperature (since 1864) were studied on a decadal time scale by Gaussian filtering technique, and the significance of trends on the 0.05 level were studied by the Mann-Kendall test. During the period no significant trend in annual precipitation was detected. The maximum value was in the 1920s and the minimum value in the 1910s. Annual mean temperature, as well as seasonal means for winter and spring, has increased significantly since 1864, while no significant trends were detected in the summer and autumn means. Concerning annual temperature the classical temperature optimum in the 1930s was surpassed by the 1990s. This is true also in the winter and spring seasons while in autumn the maximum of the 1930s was surpassed already in the 1950s. However, in summer the temperature optimum of the 1930s has still not been exceeded.

By adopting a sinus model including the first Fourier component, trends and variations in climatological periods as well as heat and frost sums were studied. The frost free period has increased since 1864 by 13 days per 100 years when adopting a linear trend line. Earlier passing date (exceeding 0 °C) in spring is the main reason for the increase. The length of the growth season increased up to the 1950s. Annual heat sum

shows a linear increase of about 103 day-degrees per 100 years while annual frost sum varies considerably from period to period, not fitting a linear model.

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Annex

The analysis of climate in the Atndalen Valley in this article is based on the data for the standard normal period in meteorology, 1961–1990. The research and monitoring data from the Atna watercourse reported in the other articles in this volume, however, largely covers the period 1986–1998. As climate undergoes decadal variations, mean values for the two periods

Table A1. Mean monthly and annual precipitation (mm) at three weather stations in the Atna watershed during 1986–1998.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Des	Year
Atndalen–Rønningen	30	21	18	21	38	75	66	79	49	41	31	31	498
Atnsjøen	31	25	21	23	39	79	75	89	59	46	34	31	552
Atndalen–Eriksrud	23	19	17	18	43	73	69	87	55	42	25	24	495

Table A2. Mean monthly and annual temperature (°C) at the weather station Sørneset and at three weather stations (*) in the vicinity of the Atna watershed during 1986–1998.

	m a.s.l.	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Des	Year
Kjøremsgrende*	626	−6.6	−6.1	−3.1	0.6	6.2	10.3	12.5	11.1	6.6	1.8	−3.8	−6.4	1.9
Sørneset	739	−7.8	−6.7	−3.8	−0.4	5.3	9.8	11.7	10.4	6.1	1.3	−4.5	−7.6	1.2
Venabu*	940	−7.7	−7.8	−5.6	−2.1	4.2	8.9	11.1	9.4	4.7	−0.1	−5.1	−7.2	0.2
Fokstua II*	974	−6.7	−7.2	−5.3	−2.1	3.7	8.1	10.4	9.0	4.6	0.2	−4.6	−6.4	0.3

are not expected to be equal. In order to provide climate data related to the other articles and to facilitate easy comparison, selected climate data for the period 1986–1998 are presented in Tables A1–A3.

During the reference period 1986–1998 Atndalen received slightly more precipitation than the standard normal period (Table A1). The annual differences were 5–28 mm, varying among stations. The largest monthly differences occurred in August

The winters of the 1990s were substantially milder than most of the winters during the standard normal period, 1961–1990 (Table A2). In January and February temperatures were 2.1 °C and 1.7 °C above the normal period. This contributes strongly to the higher annual mean temperature at Sørneset (1.2 °C) in the reference period compared with the standard normal period (0.7 °C).

A sinus model including the first order Fourier component was used as a tool for the regeneration of smoothed daily mean temperatures (Grimnes & Nissen, 2003). The model input was monthly mean temperatures at Sørneset during the common reference of this volume, 1986–1998 and the standard normal period 1961–1990. The results are put together in Table A3 enabling easy comparison.

Table A3. Passing dates, heat and frost sums for the period 1986–1998, and for the standard normal period 1961–1990, based on data from weather station Sørneset.

	1986–1998	1961–1990
Mid day of winter	9 January	17 January
Mid day of spring	21 April	19 April
Mid day of summer	20 July	19 July
Mid day of autumn	12 October	17 October
Passing point of freezing in spring	13 April	15 April
Passing point of freezing in autumn	18 October	21 October
Length of the frost period	177 days	175 days
Length of the frost free period	188 days	190 days
Start of the growth season ($\geq 5^{\circ}\text{C}$)	14 May	13 May
End of the growth season ($< 5^{\circ}\text{C}$)	22 September	24 September
Length of the growth season	130 days	133 days
Length of the hibernation	235 days	232 days
Annual heat sum	1220 day-degrees	1219 day-degrees
Annual frost sum	933 day-degrees	1097 day-degrees



Hydrology of Lake Atnsjøen and River Atna

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Key words: hydrology, Lake Atnsjøen, River Atna, reference basin

Abstract

The hydrological investigations in the Atna basin started in 1917 with discharge measurements at the outlet of Lake Atnsjøen. Ice data are available from the lake since 1950 and water temperature data from 1980. With the start of the FORSKREF program in 1986 the number of hydrological stations increased substantially and included also snow measurements. During the FORSKREF period 1986–98 the annual mean discharge was 8% lower than during the normal period 1931–60. The annual flood is highest during the snow melt in spring, an exception was 1987 when a rain flood in October was the annual high. The spring flood in early June 1995 was the largest ever recorded and had a 100–200 year return period. The water temperature is low above tree-line at 1000 m a. s. l., rarely exceeding 7–8 °C. The temperature increases gradually with decreasing altitude and is periodically above 15 °C at 400 m a. s. l. The Atna Lake is an important heat source for the river downstream. In this lake, wind mixing normally prevents the development of a strong summer thermocline. The lake usually freezes over in late November and has a stable ice cover of 50–90 cm thickness in early spring. The ice normally breaks up in late May; thus the mean ice-covered period is 6 months. The ice cover on the river is less stable and rather large ice-runs are common on the lower part of River Atna. The snow measurements are carried out in April in a small subbasin between 800 and 1200 m a. s. l. The snow cover is unevenly distributed due to strong wind transport, but the pattern is more or less the same from one season to another. The mean snow accumulation in this basin is equivalent to 205 mm of precipitation.

Introduction

In order to understand the dynamics and variation in the aquatic ecosystems, information on the hydrology of the watershed is crucial. In particular are time series data important in order to unravel the natural variations. The hydrological investigations in the Atna watershed started as early as 1917 with discharge recordings at the outlet of Lake Atnsjøen. At this location, good quality data have been collected since 1917. A couple of other locations in the watershed have provided less reliable data as the stations have had numerous breakdowns. Through the same period, observations have been made of ice cover. Since the

1980s, water temperatures in the lake and river, and snow depth have also been recorded.

The purpose with this paper is (a) to present a general picture of the hydrology of the Atna basin and (b) to explore in more detail the variables that are of special relevance to the other papers of this volume. All the primary data referred to are stored and are available from the hydrological database HYDRA II that is operated by the Water Resources and Energy Directorate (NVE).

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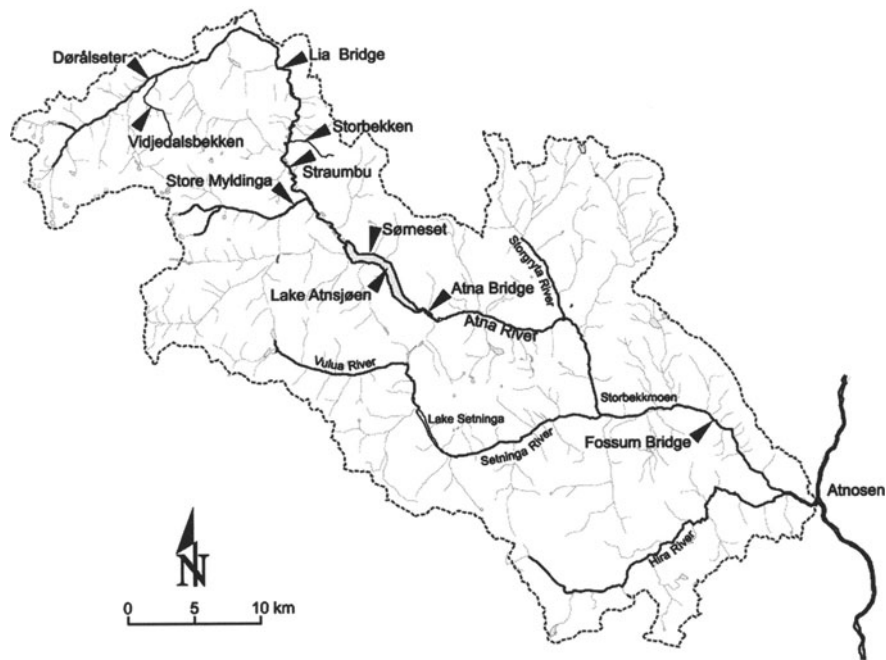


Figure 1. The Atna catchment area with hydrological measurement sites.

Table 1. Discharge data from the Lake Atnsjøen outlet.

Year	Maximum ($\text{m}^3 \text{s}^{-1}$)	Date	Minimum ($\text{m}^3 \text{s}^{-1}$)	Date	Annual mean ($\text{m}^3 \text{s}^{-1}$)
1986	54.3	6.5	1.45	19.3	8.6
1987	71.6	17.10	1.53	12.4	12.4
1988	81.7	31.5	1.80	1.4	11.9
1989	37.4	25.5	2.00	4.3	9.0
1990	94.9	22.6	2.10	14.3	10.7
1991	42.8	20.6	1.45	5.3	7.5
1992	68.7	24.5	1.83	10.4	8.6
1993	54.3	4.5	1.62	30.3	9.8
1994	42.1	7.6	1.15	23.4	8.6
1995	181.6	1.6	1.37	31.12	9.4
1996	67.5	19.6	0.76	5.4	7.5
1997	68.7	9.6	1.27	30.3	8.9
1998	66.3	10.6	1.60	17.3	10.4

Material and methods

Discharge

The dataset on discharge at the outlet of Lake Atnsjøen (station no. 2.32; Fig. 1; Table 1) represents one of the longest and best discharge series from un-

regulated catchments in Eastern Norway. Manually recorded water levels provided the basis for discharge calculations up to 1985 when a limnigraph was installed. In 1990 a datalogger was installed with direct communication to NVE in Oslo.

Temperatures

The locations of the temperature measuring stations are also shown in Figure 1. Temperature measurements of the water leaving Lake Atnsjøen (station no. 2.700; Atna Bridge), and temperature profiles from the lake itself were started in June 1980 as part of a heat balance project sponsored by the Norwegian Hydrological Committee (Hansen and Tvede 1982). In that project, current measurements were made during the summer in the northern part of the lake (Dypdal 1981), and detailed measurements were made in the inflow lead in spring 1982 (unpublished data). From 1980 a mercury thermometer was used, but in 1984 a datalogger was installed. From 1986 the number of stations in the water temperature network was expanded (Fig. 1; Table 2).

There are some gaps in the data series, partly due to loss of dataloggers, malfunctioning, or dataloggers lying dry or frozen into the ice. The latter was a particular problem both at Fossum Bridge and in Storbeekken.



Figure 2. The Lia Bridge station in the upper part of the River Atna (cf. Fig. 1).

The number of degree days for the water during the growth season is an important parameter for biological processes. The degree day totals have been calculated for each year at Atna Bridge based on the periods with daily mean temperatures exceeding minimum temperatures of 4 and 7 °C, respectively.

Ice conditions

From 1917 to 1980 the water level observer made notes on the freezing over and subsequent ice break-up on Lake Atnsjøen. This has produced a good quality data series, although there are numerous gaps in the recordings up to 1953. The observer's instructions stipulated that the ice conditions visible from the water level gauge should be reported, which means these notes only refer to the lower end of the lake.

In 1980 mapping of the whole lake was started. Since then the observer, who lives at Sørnesset, has drawn the ice cover limits on the maps and classified

Table 2. Water temperature stations in the Atna basin (cf. Fig. 1). Asterix indicates profile measurements with loggers 1980–83 and 1987. Manual measurements in March and August every year 1980–98.

Name of station	Station number	Years with data (not all are complete)	Altitude m a.s.l.
Vidjedalsbekken	2.708	1988, 1993–94, 1997	1115
Dørålseter	2.707	1988	1010
Lia Bridge	2.706	1987, 1989–90, 1992–	758
Storbekken	2.705	1986–	780
Atna upstream	2.702	1984–87	705
Myldinga			
Store Myldinga	2.703	1984–87	705
Atna Lake, lake profiles	2.699	1980–*	701
Atna Bridge	2.700	1980–	700
Fossum Bridge	2.704	1986–	420

it into four categories: 'Incipient ice formation', 'Ice-covered, but not walkable', 'ice-covered and walkable', and 'drifting ice floes'. In addition, the ice was classified as snow-covered or bare, and open leads were also plotted. The observer was required to draw a new map whenever the ice conditions changed significantly, and in any case once a month. In practice this resulted each winter in 3–5 maps, for November, December, May and June, and only one map for the period January to April.

Ice thickness is recorded each time a temperature profile is measured in March or April. This is assumed to closely approximate the maximum thickness attained in that winter. Since the winter of 1987–88, ice thickness measurements have also been made twice a month at a point right outside Sørnesset. A fixed apparatus was used which is now standard for NVE's permanent ice measuring stations (cf. Adams et al. 1986).

Systematic mapping of ice conditions in the river has not been carried out, but notes have been made during winter surveys.

Snow cover

Measurements of snow-depth and density started in 1987 and have been repeated in April each year. A small sub-basin named Storbekken was selected because this basin was already chosen for detailed investigations on water chemistry (Blakar et al., 1997). A traditional depth probing method is employed along

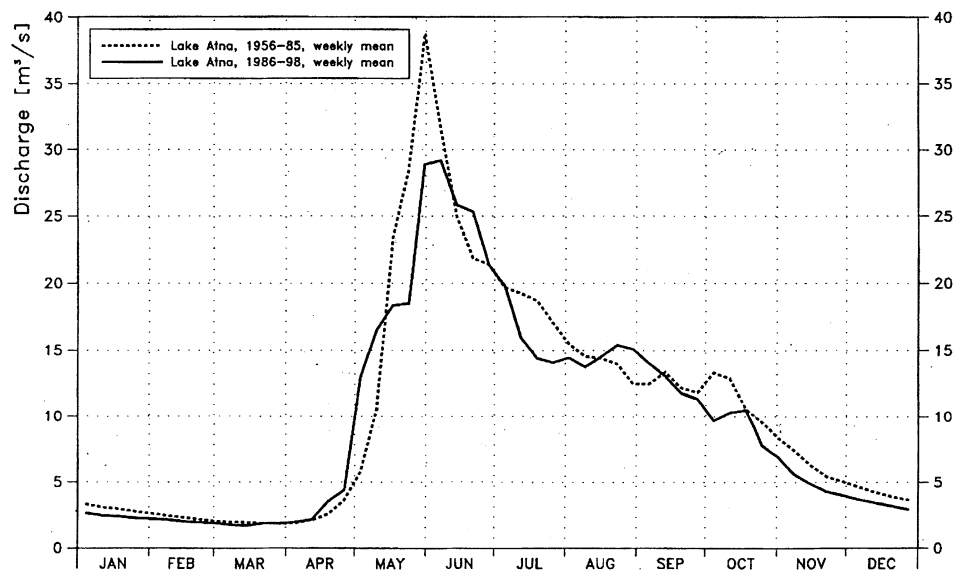


Figure 3. Average water discharge at the outlet of Lake Atnsjøen for the reference period 1956–85 and for the investigation period 1986–98.

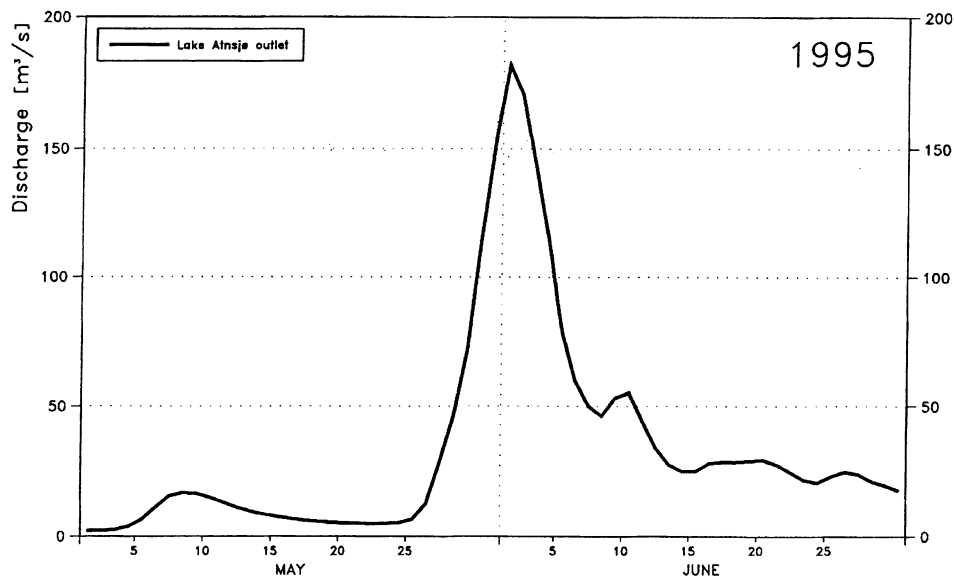


Figure 4. Water discharge at the outlet of Lake Atnsjøen during the large spring flood in May–June 1995.

fixed transects with measurements taken at 800 m and successive 100 m contours up slope. To measure snow density, pits are dug and snow cores taken from the exposed profile and weighed. The whole Storbekken sub-basin of 6.5 km² is covered by measurements, except for the area above 1200 m. This area is the southern side of the Eirikshø mountain, where the terrain is very steep and mostly swept bare of snow by the wind.

The discharge station at Fossum Bridge on River Atna's lower reach (no. 2.457; Fig. 1) is also in

continuous operation. This station may, however, be exposed to massive ice jams during winter, and has broken down a few times, particularly during 1985–87 and 1993–94. The data quality is therefore inferior to those from Lake Atnsjøen. NVE has also operated a summer discharge station at Lia Bridge (Fig. 2), in connection with sediment transport measurements, but this too has had a number of breakdowns. In this paper, all further reference to discharge in the Atna basin is therefore based on the Lake Atnsjøen station.

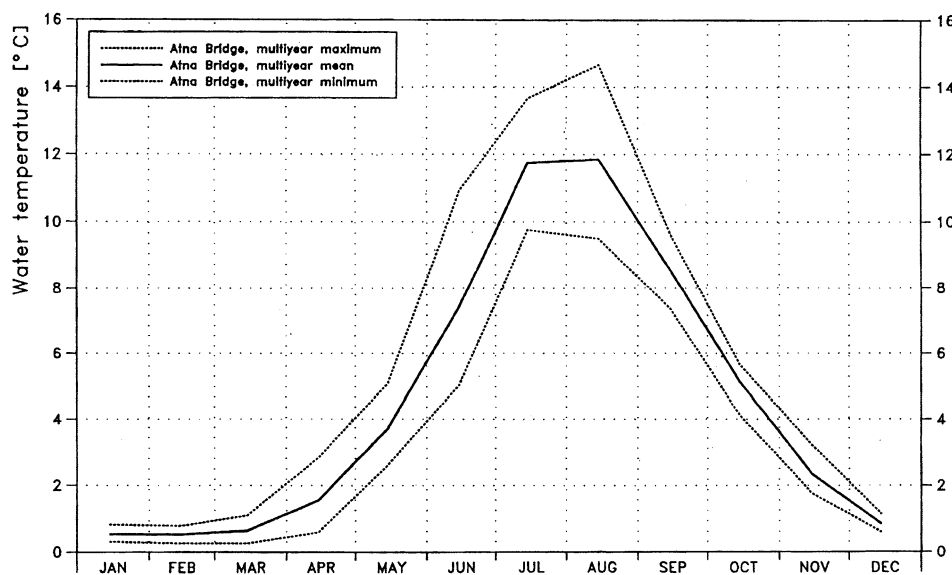


Figure 5. Mean water temperatures at Atna Bridge for the investigation period 1986–98.

Results and discussion

Discharge

Mean values for the period 1986–98

The mean discharge for the 30-year ‘normal’ period of 1931–60 was $10.32 \text{ m}^3 \text{ s}^{-1}$ while for 1986–98 it was $9.5 \text{ m}^3 \text{ s}^{-1}$. The difference is very small, especially when one takes into account the uncertainties inherent in the manual readings during the ‘normal’ period. Altogether seven years (1986, 1989 and 1991–97) were drier than the ‘normal’, while 1987, 1988 and 1990 were wetter. The driest years were 1991 and 1996 with $7.53 \text{ m}^3 \text{ s}^{-1}$ while 1987 was the wettest with $12.40 \text{ m}^3 \text{ s}^{-1}$. It may seem surprising that the annual mean for the great flood year of 1995 (cf. Fig. 4) was below the normal value. The flood volume was not sufficient, however, to make up for the dry summer and autumn of that year.

The mean discharge curves for the period 1986–98 are plotted in Figure 3 along with the mean for the preceding 30-year period, 1955–85. It may be noted that 1987 was the only year since 1957 when the highest annual flood came in the autumn. In all the other years the spring flood was greatest. The autumn flood of 1987 was also unusually large all over Eastern Norway (Engen, 1988). However, high autumn discharges also do occur in other years. Winter discharge in the River Atna shows little variation from year to year. Even the unusually mild winters of 1989, 1990, 1992 and 1993 had little effect on flow during the winter months. The

reason is that the stable groundwater drainage from the large valley deposits maintains most of the winter discharge in the river.

The floods of 1995 and 1996

The spring flood at the beginning of June 1995 (Fig. 4) was quite exceptional and caused extensive and serious damage further downstream in the Glomma valley. Erichsen (1995) has included data from Lake Atnsjøen in his statistical analysis of this flood. He concluded that the flood peak had a 100–200 year return period. This corresponds well with the flood frequency curves in Tvede (1989). Characteristic for the flood was its peak intensity. First there had been unusually low flow up to 25 May, followed by a rapid rise that culminated on 2 June. By 10 June the river had returned almost to its normal level (Fig. 4).

In 1996 on 18 June there was another large flood, this time in the Atna valley upstream of the lake. At Lia Bridge the water rose to above the floor level in the instrument hut (cf. Fig. 2), even higher than during the 1995 event. Fortunately the observer was there and managed to rescue the equipment. An accurate estimate of the maximum discharge is impossible because the discharge curve is not valid for such high water levels. A figure of about $90 \text{ m}^3 \text{ s}^{-1}$ is suggested; see further discussion in Bogen (2004). The event was essentially a rainstorm flood caused by locally very heavy precipitation in the Rondane Mountains. The preceding winter had been particularly cold and the deep frost in the soil had not yet thawed out on high

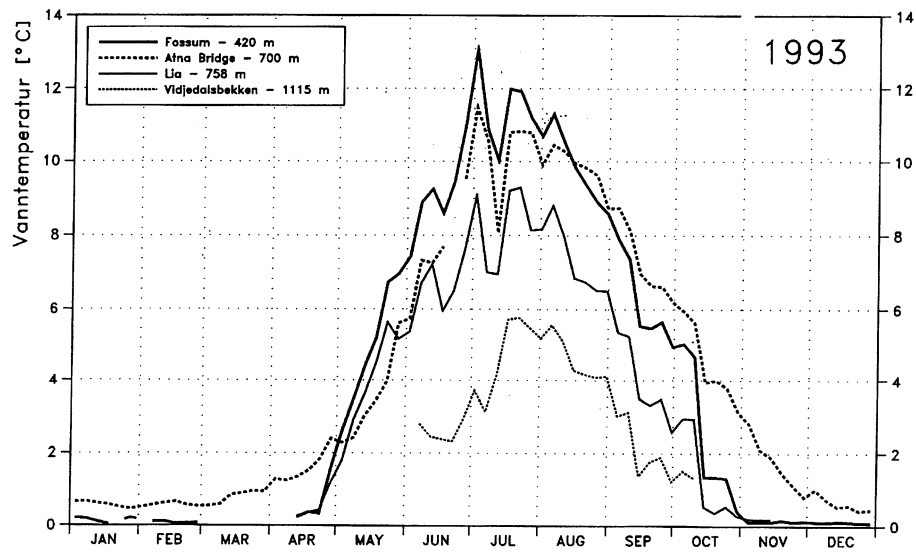


Figure 6. Water temperatures from four measurement stations during 1993.

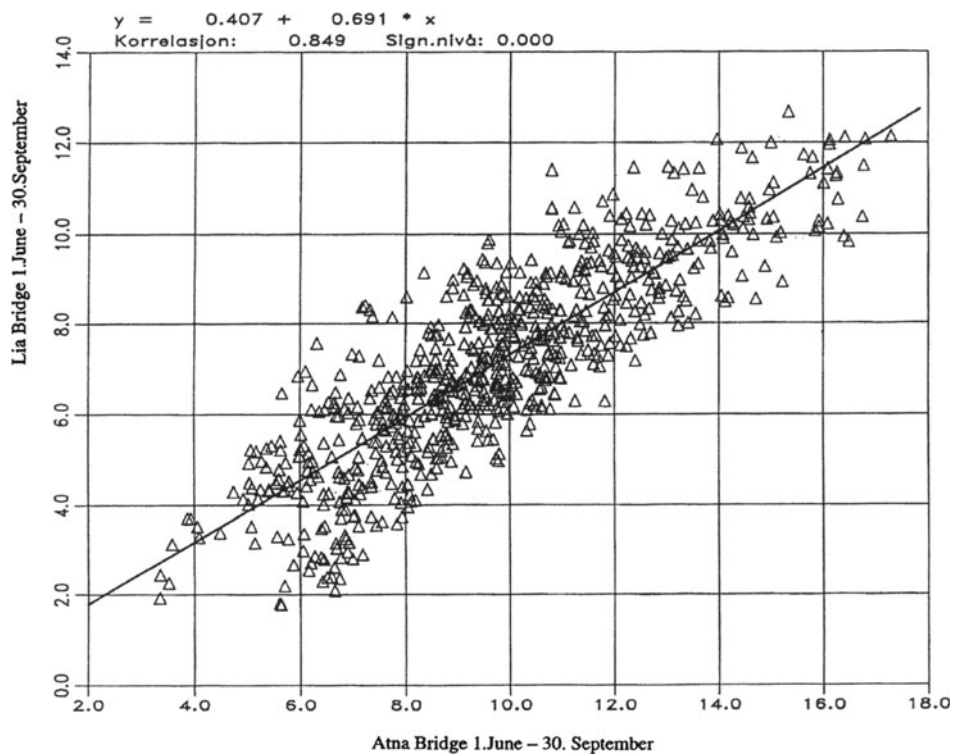


Figure 7. Correlation between daily water temperatures measured at the stations Lia Bridge (y, upstream of Lake Atnsjøen) and Atna Bridge (x, downstream of the lake). The regression $y = 0.407 + 0.691x$ is highly significant ($R = 0.849$, $p < 0.0005$).



Figure 8. Vidjedalsbekken at 1150 m a.s.l. , 8 August, 1995. Snow patches along the creek keep the water temperature low also in sunny summer weather.

ground. This may have contributed to the severity of the flood by promoting surface runoff. Lake Atnsjøen reduced the flood peak significantly; the maximum discharge measured at the outflow was $67,5 \text{ m}^3 \text{ s}^{-1}$ on 19 June.

Water temperature

Mean and extreme values for 1986–98

Figure 5 presents the monthly mean temperature curves for the station Atna Bridge. July and August are normally the warmest months, both with a mean water temperature of 11.9°C . It should be noted that year to year variations in the ice-free period are smallest in the fall. With regard to extreme temperatures the highest daily mean recorded at this station was 17.5°C on 1 July 1986, but the water was almost as warm on 5 August 1991 and 4 August 1994. On average though, the late summer of 1997 was decidedly the warmest with mean values for July, August and September being the highest recorded in the whole measurement period.

Individual years

Figure 6 shows a more detailed plot for the year 1993. When analysing this figure and similar plots for the other years, the following trends are seen to characterize the water temperature in the Atna basin:

- There is a distinct temperature development from the alpine to the lower part of the river system. In

the lower reaches the summer temperature is periodically above 15°C , while above the tree limit at 1000 m a. s. l. it rarely exceeds $7\text{--}8^\circ\text{C}$.

- Upstream of Lake Atnsjøen the river temperature scarcely reaches 10°C except for short periods in July and August. The warmest water temperatures often occur later in summer above the lake than downstream of the lake.
- Lake Atnsjøen has a year-round effect of warming and levelling out the water temperature downstream. However, in parts of May and June the inflowing water may be a little warmer than the outflow.
- The correlation between water temperatures is good between the stations above Lake Atnsjøen, and less so between stations above and below the lake (cf. Fig. 7).

Relationship between air and water temperatures and snow conditions

Fourteen years of data collection in the Atna water course have provided a good basis for examining more closely the relationships between water temperature, climate and ice and snow conditions in the catchment area. Figure 8 illustrates the delaying effect on the summer rise in water temperature caused by snow remaining near the river channels.

In Figure 9 the monthly means for water temperature in July at Atna bridge have been plotted along

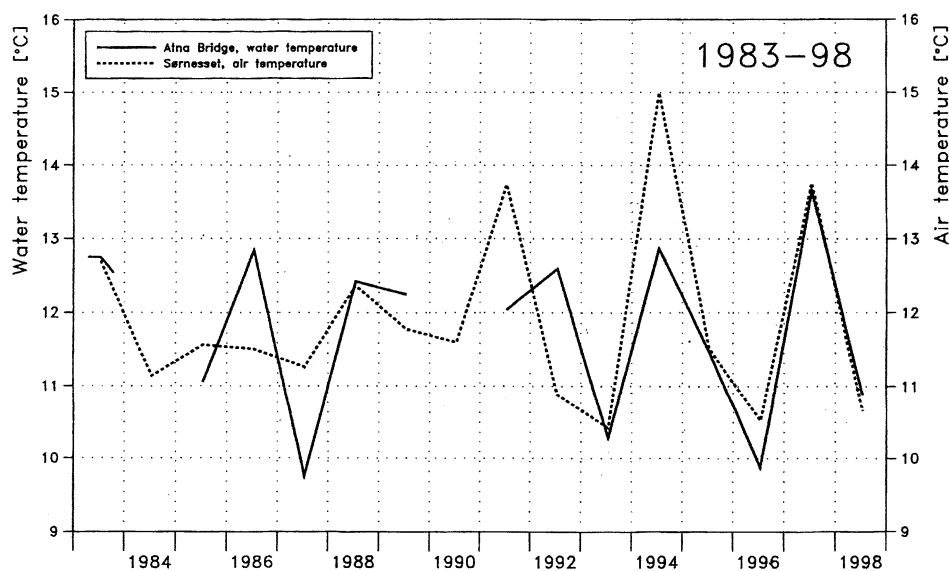


Figure 9. Monthly mean air temperature at Sørnesset (750 m a.s.l.), and water temperature at Atna Bridge (695 m a.s.l.) for the period 1983–98.

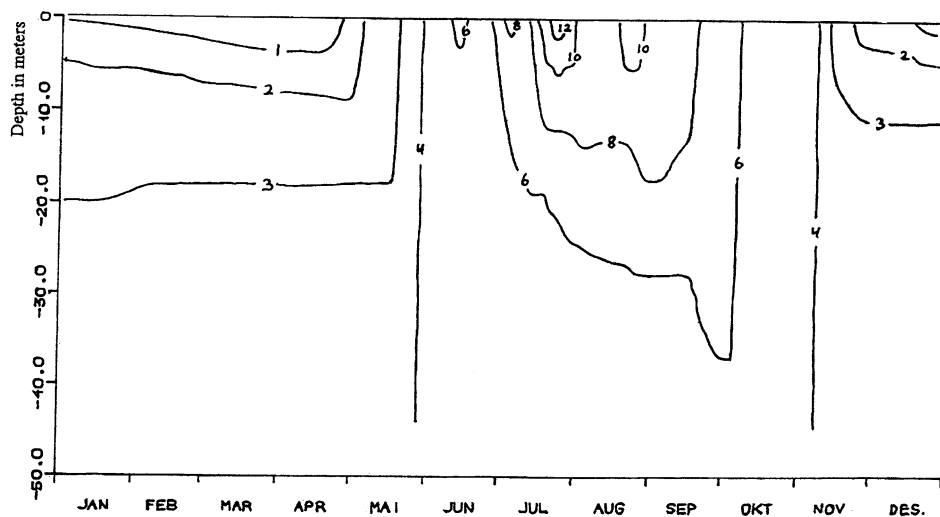


Figure 10. Temperature isopleths from Lake Atnsjøen in 1987. Measurements were made by thermistors connected to a data logger.

with the air temperature data at Sørnesset (see description of the meteorological stations; Grimnes & Nordli, 2004). There is a close correspondence between water and air temperature variations, though there are deviations. In particular, July 1992 stands out with a relatively high water temperature despite prolonged cool weather. This may probably be explained by the shallow snow accumulation (as measured in April that year; Table 5). This implies that nearly all the snow in the mountains would have melted during the course of June so that by July the meltwater contribution to the discharge in Atna was much less than normal. A similar plot for monthly mean values in June shows

much larger deviations between the air and the water temperatures, indicating that remaining snow and ice have a larger influence in June than in July.

Degree day totals at Atna Bridge

The degree day totals based on minimum temperatures of 4 and 7 °C, respectively, are shown in Table 3. This reveals that during the recorded period, the 1987 growth season was the coldest with only 87 days exceeding 7 °C, reaching 801 degree days. The warmest season was 1992 with 129 days above 7 °C, yielding 1357 degree days. Based on a minimum temperature of 4 °C, 1987 is still the coldest growth season, but

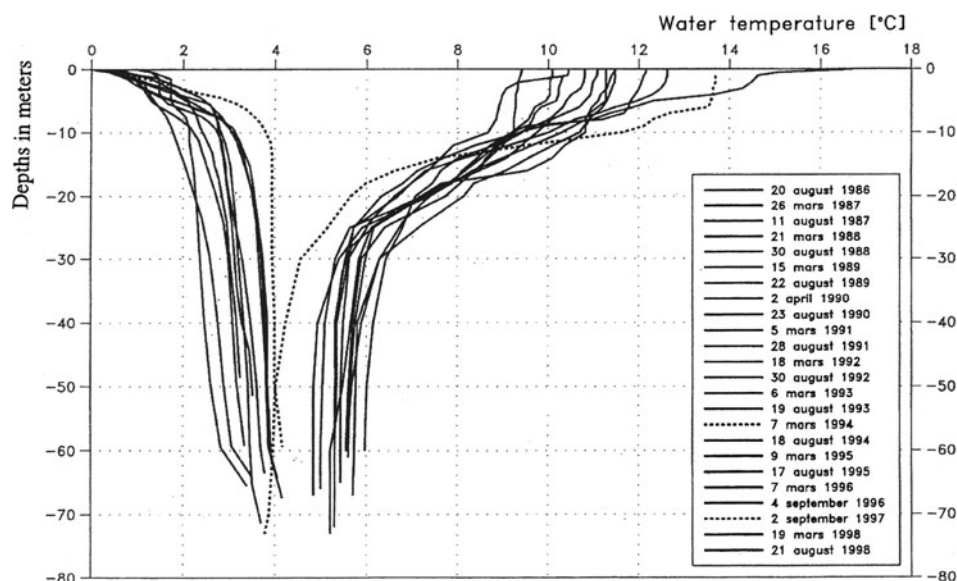


Figure 11. Vertical temperature profiles measured annually in spring and in late summer in Lake Atnsjøen.

Table 3. Degree days calculated from number of days with mean temperatures above 4 and 7 °C at the Atna Bridge station, 1986–98.

Year	>4 °C degree days	Days in period	>7 °C degree days	Days in period
1986	1394	153	1114	100
1987	1213	163	801	87
1988	1475	155	1189	105
1989	1396	169	1121	108
1990	No data		No data	
1991	1615	186	1188	106
1992	1522	161	1357	129
1993	1221	149	933	99
1994	1388	151	1073	95
1995	1419	149	1150	100
1996	1255	144	951	89
1997	1560	160	1260	104
1998	1362	163	1062	109
Mean	1400	157	1100	103

1991 becomes the warmest and has the longest period above the boundary value.

Temperature profiles in Lake Atnsjøen

There were hourly recordings (with dataloggers) of water temperatures in the lake in 1980–83 and in 1987 (Table 2). Isopleth diagrams were plotted based on

Table 4. Thickness (cm) of ice and snow on Lake Atnsjøen, 1981–98.

Date	Snow	Snow ice	Black ice	Total ice thickness
18.03.81	12	4	82	86
19.04.82	0	23	32	55
18.04.84	0	0	77	77
26.03.87	30	2	62	64
21.03.88	41	1	54	55
15.03.89	6	2	65	67 (three layers)
02.04.90	12	8	38	46
05.03.91	7	14	54	68
18.03.92	7	4	61	65
06.03.93	10	29	55	84
07.03.94	28	12	50	62
09.03.95	27	10	43	53
07.03.96	13	0	90	90
1997				No data
19.03.98	0	12	45	57

these data, in Fig. 10 the diagram for 1987 is presented as an example, while the other years were published in Tvede (1989).

The manual readings from both winter and summer measurements are shown in Figure 11. Variations are relatively small between winters, because of the continuous ice cover. Lakes with less stable ice conditions will experience larger variations in winter temper-

Table 5. Snow measurements in the Storbekken catchment.

Date	Volum of water (mill. m ³)	Mean density (kg dm ⁻³)	Mean accumulated precipitation (mm)
22.04.1987	1.57	0.35	240
12.04.1988	1.85	0.35	282
12.04.1989	1.36	0.40	208
19.04.1990	1.57	0.40	240
05.04.1991	1.09	0.39	166
23.04.1992	0.87	0.36	133
14.04.1993	1.47	0.40	224
19.04.1994	1.56	0.34	238
19.04.1995	1.66	0.37	253
16.04.1996	0.53	0.36	81
16.04.1997	0.87	0.36	133
21.04.1998	1.73	0.37	264
Mean	1.34	0.37	205

atures. The warmest winter profile was recorded in March 1994. The record early freezing over which stopped the cooling of the water masses early during autumn 1993 (Fig. 12) explains this. The August profiles also show only relatively small variations from year to year below about 10 m depth. Variations are somewhat greater in the upper 10 m. Following the exceptionally warm summer in Southern Norway in 1997, the profile from August this year is an exception. A strong thermocline probably developed early, preventing the mixing of warmer surface water with the hypolimnic water, which consequently remained cooler than usual also in late August. In some summers, Lake Atnsjøen does not develop a pronounced thermocline, which is otherwise typical in many lowland lakes in Eastern Norway. The reason is Lake Atnsjøen's exposure to the northwesterly winds. Figure 10 shows only weak thermal layering in the lake during the summer 1987, though in some years such as 1980 and 1982, it had developed significantly by late summer.

Ice and snow conditions

Freezing over and ice break-up

Figure 12 shows the ice-cover periods from 1953–54 to 1997–98. For the reference normal period of 1954–85 the median date for the initiation of the freezing is 17 November with complete ice cover by 24 Novem-

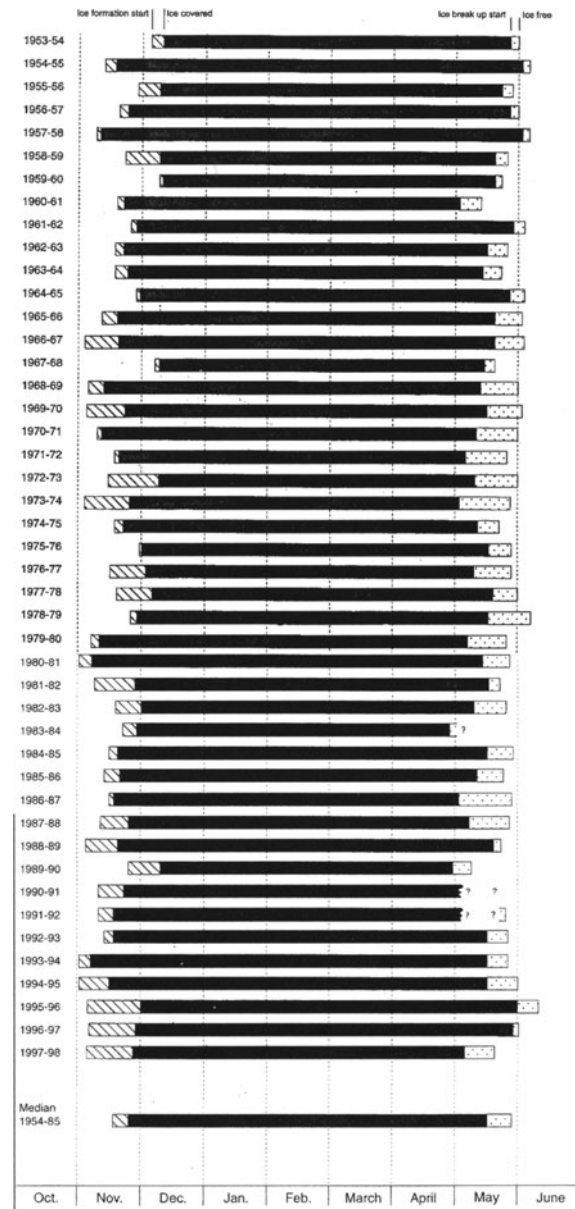


Figure 12. The duration of ice-cover on the lower part of Lake Atnsjøen for the winters 1953–98.

ber, while the commencement date for ice break-up is 15 May with the lake ice-free on 27 May. During the period 1986–98 freezing has begun about a week earlier while the timing of break-up has not changed. It was noted that the freezing over in autumn 1993 was the earliest observed, and the 1996 ice break-up the latest.



Figure 13. Ice conditions in River Atna at Gammelgarden, 16 April, 1996. The ice is formed by a static process and has a smooth surface



Figure 14. Ice conditions in River Atna at Fossum, 23 April, 1987. The ice has been formed by a dynamic process from drifting frazil and has an uneven surface.

Ice thickness

During the period 1981 to 1998, ice thickness on Lake Atnsjøen varied between 46 and 90 cm and nearly all the ice was black ice (Table 4). Ice thickness will always vary somewhat from place to place over the lake surface and 9 measurements taken at points scattered across the lake on 18 March 1981 revealed a range from 75 to 86 cm.

Ice conditions in the river

Above Lake Atnsjøen the river usually has a stable ice cover from November to April (Fig. 13). Ice forms statically, in the same way as on a lake. In a few areas there is open water or weak ice where groundwater springs with a temperature of 2–3 °C seeps out. During April the ice gradually breaks up and the river is normally ice-free before the onset of the spring flood. No large-scale ice floes have been noted along this reach.



Figure 15. Ice conditions in Storbekken, 15 April, 1996. Following an unusually cold winter the ice has filled up the whole bed of the creek.



Figure 16. Snow distribution in the Rondane Mountains after a winter with much snow (12 April, 1988, upper photo) and after a winter with little snow (15 April, 1996, lower photo).

Below Lake Atnsjøen the river ice conditions are different (Fig. 14). Freezing over takes place by a so-called a dynamic process. Frazil ice forms in the rapids and builds up into ice dams downstream. Between these ice dams the river gradually freezes over statically. The ice dams are sometimes unstable and, during the early winter, ice runs can result if one or more of the ice dams fail. At some places, including Fossum Bridge, ice from several such winter ice runs may accumulate to create barriers, raising the water level. This makes the winter discharge values from this locality less reliable. Some years large ice runs have been released, causing swiftly rising water levels. For example, destructive ice runs were reported from the lower Atna in April 1987 and 1988. The damage was caused by ice pushed across arable land and by soil erosion by the floodwater where it was forced up and out of the river channel. Riparian vegetation may also suffer from the ice, most commonly by the bark being stripped off tree trunks.

The winter of 1995–96 was an unusually hard ice winter in Southern Norway and the River Atna basin was no exception. Persistent cold with little snowfall allowed the frost to penetrate exceptionally deep and very many stream channels became filled with compact ice. This is ice formed when groundwater is forced out into the channels because of the deep frost table in the surroundings. When these channels became full, large icings formed beyond the channel

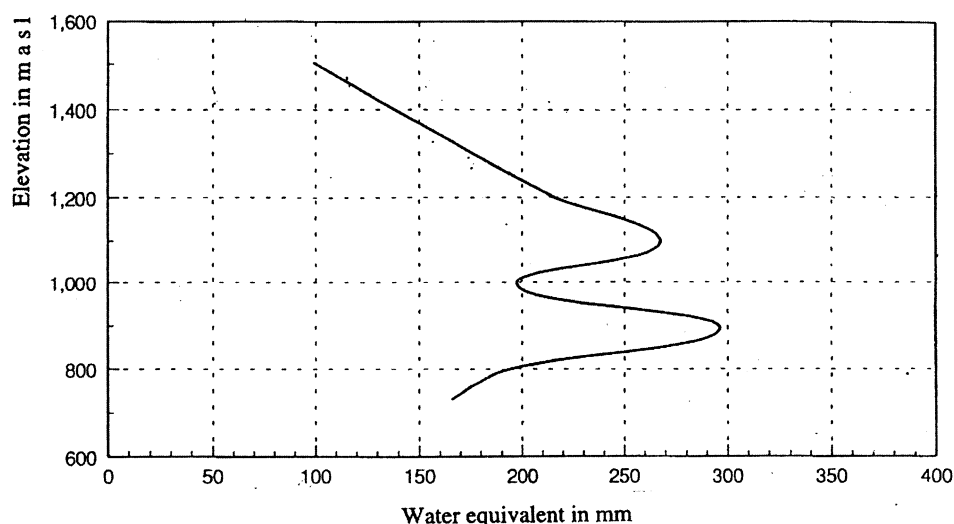


Figure 17. Snow distribution with altitude in the Storbekken basin 14 April, 1993. The uneven distribution in this small basin is explained by strong wind drift of the snow.

banks. Figure 15 shows such conditions in Storbekken in April 1996.

Snow conditions

The main findings concerning snow conditions in the Storbekken sub-basin from the period 1987–98 are summarised in Table 5. Maximum snow depth was recorded in spring 1988 and minimum in 1996 (Fig. 16). An analysis on the relationship between precipitation recorded at the Sørneset weather station and the accumulation of snow in the Storbekken catchment is possible, but would require that the first day of snow accumulation had been recorded each year.

The distribution of snow throughout the catchment is very uneven due to drifting and differences in the vegetation and terrain. Exposed areas can be virtually bare while nearby stream courses and hollows may collect snow patches 3–4 m thick. Figure 17 shows the amount of snow related to altitude in 1993. There is a maximum around 900 m altitude, which coincides with the sub-alpine birch forest zone. Clearly this woodland traps snow blown down from more open alpine areas. This distribution is more or less repeated every year. However, after winters with little wind, as in 1996, the variation with altitude is less. The snow measurements in the Storbekken catchment have been compared with snow distribution data from satellite images for April 1996. This is a continuing project that also may give us an idea about how representative the Storbekken basin is compared to the rest of the Atna basin.

Acknowledgements

The FORSKREF program has been financed by a mixture of research grants from the various sources and resources allocated by the participating institutions. This is described in more detail otherwise in this publication. However, the main reasons why this program has been able to continue, also through years of financial constrain, is the personal initiatives and enthusiasm shown by the various researchers who have participated. Indispensable assistance was provided by the local observers in the Atna valley. In particular should be mentioned Odd Brænd who looked after the water level gauge and noted the dates for the ice freeze-up and break-up on Lake Atnsjøen during 62 years from 1937 to his death in 1999.

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Erosion and sediment yield in the Atna river basin

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Key words: erosion processes, sediment yield, suspended sediment transport, particulate organic matter (POM), mountain catchment, Norway

Abstract

Variability in suspended sediment transport and its relation to erosion processes in two different catchments within the Atna river basin are discussed on the basis of 14 years of data collection. The upper Atna catchment is a headwater system covering 157 km². Extensive glacifluvial deposits are the main sediment source of the river. Sediment transport in the upper Atna during 1988–2001 ranged from 79.4 t to 13,200 t. The extreme upper value was due to an extreme rainflood in 1996. Suspended sediment concentrations varied from less than 1.0 mg l⁻¹ to a maximum of 2023.8 mg l⁻¹. There was no correlation between water discharge and suspended sediment concentration. Despite a fairly constant volume of total runoff, sediment concentrations remained at a high level during the first years after extreme floods, and then decreased over several more years.

The complicated pattern of short term and long term variations in suspended sediment concentration and load was explained in terms of channel changes and variations in exposure of the sedimentary deposits to fluvial erosion.

The catchment of the lower Atna drains an area of 672 km². Concentrations of inorganic suspended sediments were found to vary between <1.0 and 897 mg l⁻¹, with only a weak correlation to water discharge. The suspended sediment transport per year ranged from a minimum value of 574 t in 1991 to 60,651 t per year in 1995, the extreme flood year. The mean annual transport for all the years was 6271 t. The sediment transported in the lower Atna is derived from the same types of sources as in the upper catchment, but the sediments are supplied from a larger area. Grain size distribution analyses indicate that the transported sediments in upper Atna have a sand content of 10 to 65% compared to 2–20% in lower Atna. The transport of particulate organic matter in the upper and lower Atna catchments amounted to 9.8% and 12.6% of the total load, respectively.

Introduction

Sediment transport in rivers affects both the biota and their habitats. Possibly more than any other ecological system, river ecosystems are moulded by physical forces and their flow rates can vary dramatically even over short distances and periods (Calow & Petts, 1992). Measurements have shown that the sediment yields of Norwegian river basins range widely in character and may display extreme temporal variations. Systematic measurement of suspended sediment transport with high time resolution was initiated in glacier meltwater rivers by NVE in the late 1960s (Østrem

et al., 1975). Suspended sediment transport was shown to vary greatly, both seasonally and short-term. Similar high resolution measurements were later initiated in glacier-free rivers (Bogen, 1986). This led to the recognition of five types of sediment source area: marine clay areas, forested upland, catchments in the Arctic and mountain areas, glacier outlets, and the glacier-fed rivers (Bogen, 1996). Cultivated land may be regarded as a separate source category.

These source type areas were defined as areas where soils and processes of erosion and sediment production are essentially of the same kind. The sediment yield reflects the intensity of the processes of

erosion within a river basin. There are large differences between sediment yields of the different source type areas reflecting the intensity of these processes. However, individual rivers can also show a marked year to year variability in sediment load.

The programme of long-term measurements was started in Atna at the end of the 1980s in order to study the relationship between suspended sediment fluctuations and physical, chemical and biological processes operating in the river basin.

The objective of this paper is to discuss the longer term variability in suspended sediment transport and its relation to processes of erosion in two different catchments within the Atna river basin. Other studies of sediment transport in Atna have been carried out by Bogen (1983a,b; 1989; 1997). The Quaternary deposits and the deglaciation forms in the area have been investigated or mapped by, among others, Strøm (1956), Gjessing (1960), Sollid & Carlsen (1979) and Follestad (2001).

Study area and methods

River Atna is a tributary of River Glomma in south-eastern Norway, and its basin covers an area of 1319 km². The bedrock is almost entirely highly metamorphosed Late Precambrian quartzite (Ofteidal, 1950). A map of the Quaternary sedimentary deposits is shown in Figure 1. A thin layer of till covers about 65% of the area, glacifluvial and fluvial deposits account for a further 7%, bogs cover 5% and the remaining 23% is exposed bedrock. The tills are heavily consolidated and not very susceptible to erosion. The main sediment sources are the loosely compacted and often fine-grained glacifluvial and fluvial deposits, which are very thick in some areas and have been heavily eroded when exposed to recent fluvial activity. Large systems of terraces, eskers and more irregular meltwater landforms were deposited during the final deglaciation and subsequently eroded by the rivers throughout the postglacial period. In Dørålen valley, River Atna is now incised up to 100 m into such deposits.

The higher mountain areas are exposed to extensive frost shatter activity. However, these processes tend to produce coarse material contributing to the bed load in the rivers. The volume of fine material produced is of negligible magnitude when compared to the delivery from erosion of the overburden.

The monitoring station at Lia Bridge (Fig. 1) records drainage from the western part of the Rondane Mountains. The catchment area includes 157 km² between the tree line at 900 m a.s.l. and peaks up to 1800 m a.s.l. Most of the sediment transport recorded at the station is derived from a 9 km² area covered by extensive deposits of Pleistocene glacifluvial sediments.

The station at Fossum Bridge is situated in the lower part of River Atna (Fig. 1). The total catchment above this station is 1138 km² but Lake Atnsjøen is an efficient sediment trap and the sediments passing Fossum Bridge are supplied from the 673 km² catchment area below the lake. A large part of this catchment is covered by coniferous forests. The overburden is discontinuous and the sediment sources of a patchy nature.

Results and discussion

Sediment transport in upper Atna

Seasonal variations in particle concentration at the upper station in River Atna are shown for selected years in Figure 2. As exemplified by the 1989 data, the highest concentration occurred during the first snowmelt in spring. The following weeks the concentration decreased even when the water discharge increased. The highest water discharge in 1989 of 50 m³ s⁻¹ at Lia Bridge was during a rainflood event at the beginning of August but the measured concentrations during this incident were as low as 2–3 mg l⁻¹. During the years 1987–1994, a pattern of decreasing concentrations was observed. In 1987 the concentration exceeded 20 mg l⁻¹ in 30 samples. This was reduced to six in 1989 and five in the following year. In 1992 and 1993 there were no samples in this category, and only two in 1994. In 1990, concentration remained low except for a water discharge of moderate magnitude that triggered an erosion event during the increasing water levels. At a water discharge of 16 m³ s⁻¹, the concentration was measured to 454.3 mg l⁻¹. This is very high when compared to the annual mean concentrations for 1987–1994 which are in the range of 1.0 to 11.5 mg l⁻¹ (Table 1).

In 1995 a major flood culminated on 1 June at 100 m³ s⁻¹ at Lia Bridge (Tvede, 2004). The highest measured concentration of suspended sediment was 606.1 mg l⁻¹. Rapid snowmelt accompanied by relatively heavy rainfall was responsible and this 100-year

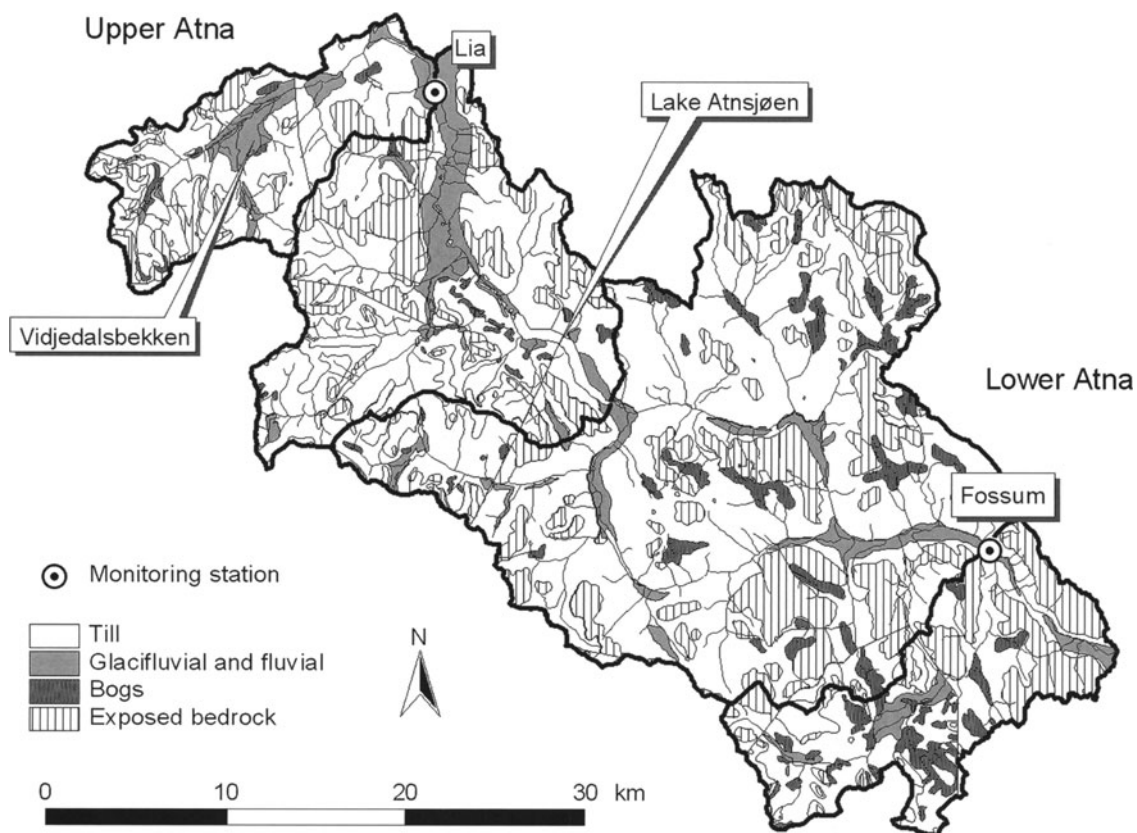


Figure 1. Quaternary deposits in the Atna catchment. River Atna is a tributary of River Glomma. Subcatchments draining to monitoring stations at Lia bru (bridge), Fossom bru and the outlet of Lake Atnsjøen are indicated. Data from Norwegian Geological Survey.

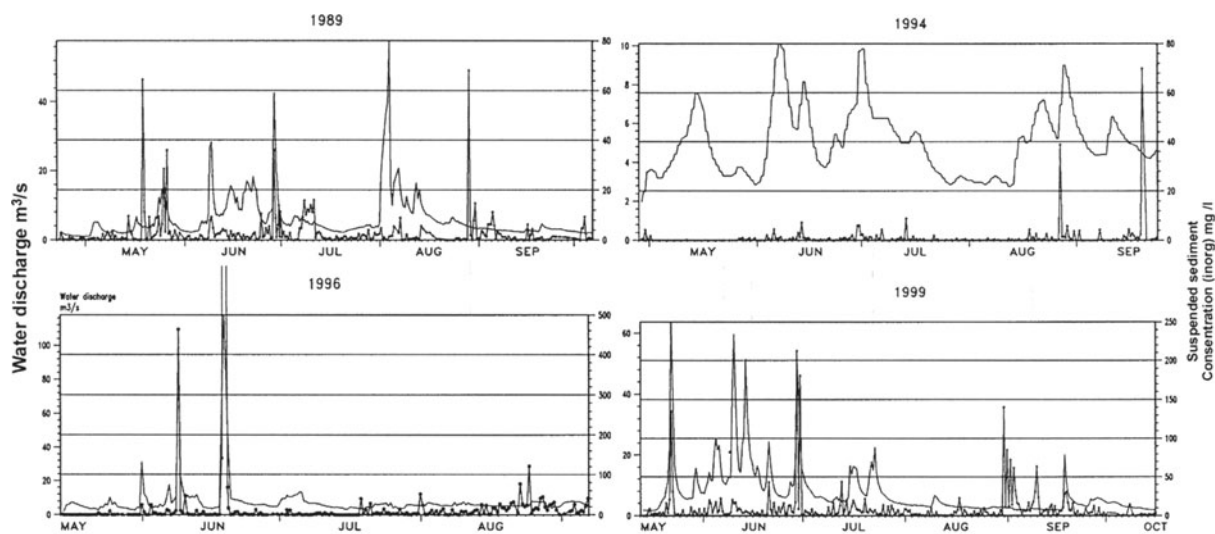


Figure 2. Suspended inorganic sediment concentrations (.....) and water discharge (—) at station Lia bru in upper Atna, in selected years.

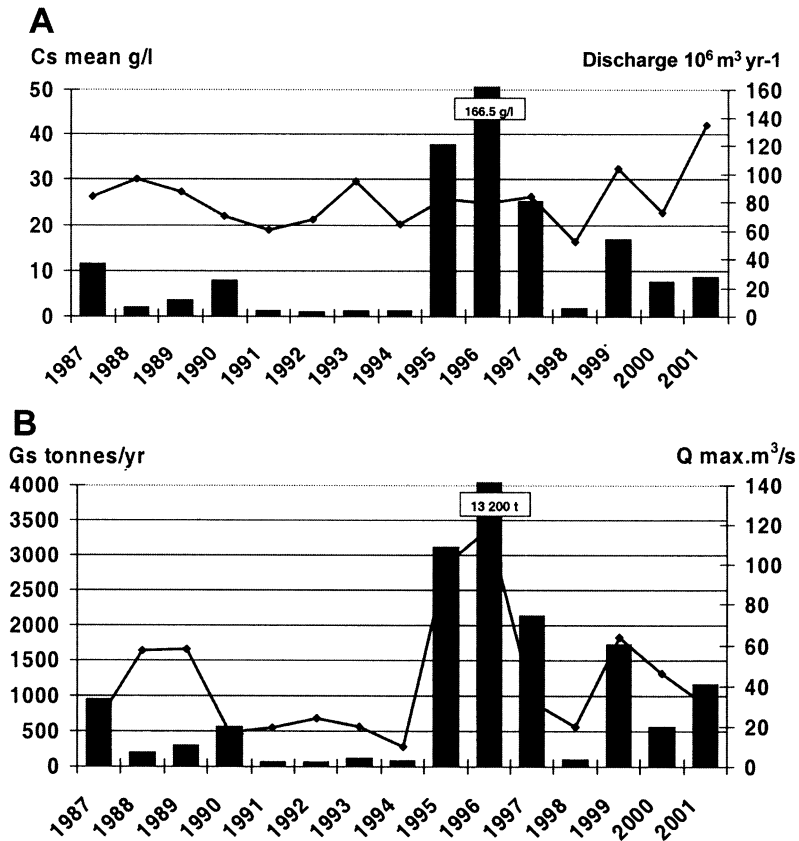


Figure 3. a: Mean annual suspended sediment concentration (Cs, g l^{-1} ; columns) and total runoff (Discharge, $10^6 \text{ m}^3 \text{ yr}^{-1}$; line) at Lia bru. b: Annual suspended sediment transport (Gs, tonnes yr^{-1} ; columns) and maximum annual water discharge (Qmax, $\text{m}^3 \text{ s}^{-1}$; lines) at Lia bru.

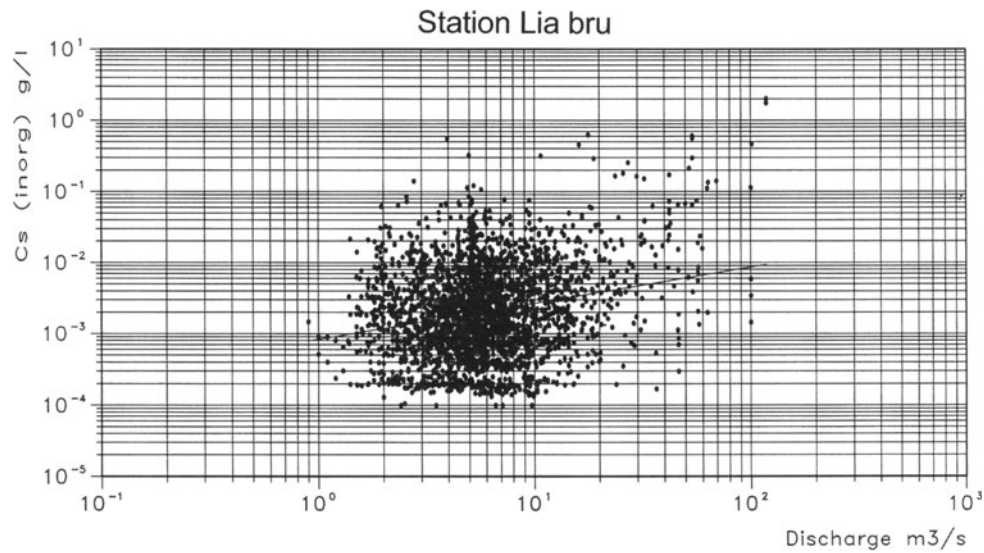


Figure 4. Regression analysis of suspended inorganic sediment concentration (Cs, g l^{-1}) vs. water discharge (Q, $\text{m}^3 \text{ s}^{-1}$), Lia bru, 1987–2001. The regression model is $Cs = 0.0008344 Q^{0.5077574}$, $r = 0.23$.

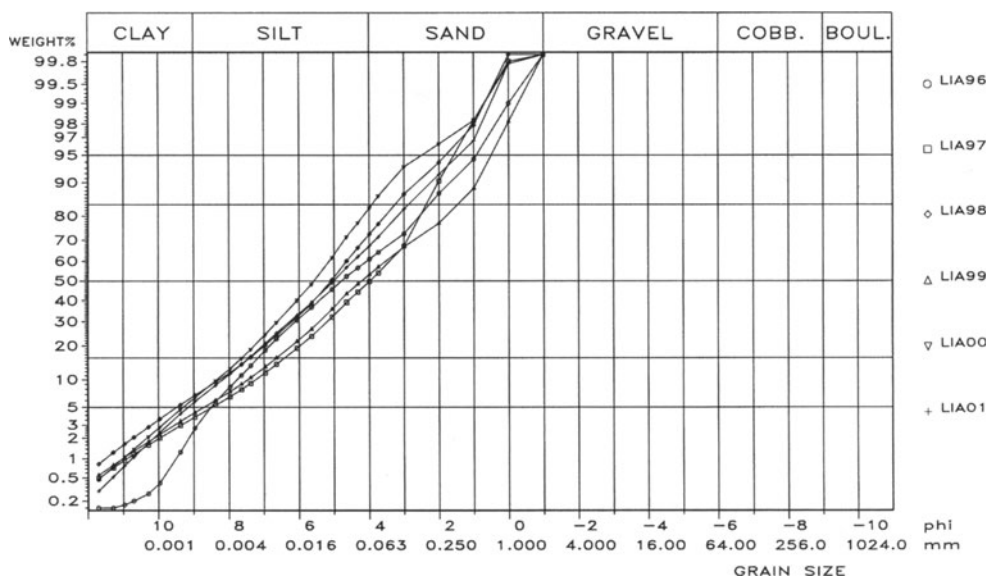


Figure 5. Mean annual grain size distribution of suspended sediment 1996–2001, Lia bru. (Each curve represents the mean of all samples in one year).

flood severely affected large areas in southern Norway. In some areas of the Glomma watershed, its magnitude corresponded to a recurrence interval of 200 years. At Lia Bridge the 1995 flood discharge was exceeded in 1996, culminating at $118 \text{ m}^3 \text{ s}^{-1}$ on 18 June, but this time the flood originated from a local rainstorm which only affected a small area of the Rondane mountains. As the total volume of the flood was only moderate, the discharge in the lower part of the river Atna was not especially high; the $128 \text{ m}^3 \text{ s}^{-1}$ recorded at Fossum Bridge on 19 June is exceeded almost every year.

At the upper station Lia Bridge, the exceptionally high maximum suspended sediment concentration of 2023.8 mg l^{-1} was measured during the 1996 flood event, while the concentration at the lower station Fossum Bridge during this event was as low as 10.9 mg l^{-1} . The very high concentration at Lia Bridge was probably due to the large amount of erosion scars created by large flood in 1995. The rainstorm did only affect a small area, but it may have been very intense. As the volume was small, the water discharge was not exceptionally high in the lower parts of the Atna catchment.

Although there were no large changes in total runoff during the years 1987–2001, the mean concentration of suspended sediment did increase after the years with the major floods when compared with the preceding years. (Fig. 3a). The number of occa-

sions when the concentration exceeded 20 mg l^{-1} also increased. In 1997 the suspended sediment concentration exceeded 20 mg l^{-1} 26 times, in 1998, 3 times, 22 times in 1999, 13 times in 2000, and 12 times in 2001. The total annual transport of inorganic suspended sediment at Lia Bridge is shown in Figure 3b and Table 1. A long-term trend seems to be present. The clear year to year variation is superimposed on a general decrease from 962 t in 1987 to 79.4 t in 1994. Large floods occurred in 1995 and 1996. During 1996 the large water discharge of $118 \text{ m}^3 \text{ s}^{-1}$ caused a huge increase in the transport rate to 13 200 t. Afterwards the transport remained at a high level but once more with the annual fluctuations displaying a gradual overall decrease. The mean transport of all the years of measurement amounts to 1624 t.

A plot of all the measured concentrations versus water discharge indicates that there is no correlation (Fig. 4). The grain size of the suspended sediments in upper Atna is fairly coarse and subject to seasonal and annual variations (Fig. 5). The amount of sand, i.e. fractions between 2 and 0.63 mm, varies from 10 to 65%. There is relatively little clay; 2.5 to 10% of the particles are smaller than 0.002 mm. The distance between the source areas and the monitoring station is relatively short and the gradient steep. There is therefore little sedimentation and the grain size of the suspended sediments to a large extent reflects the composition of the source sediments. The seasonal

Table 1. Station Lia bru, 1987–2001. Organic and inorganic total transport, % organic transport, total and maximum annual water discharge, maximum and mean annual concentration, and mean annual grain size of suspended sediments.

Year	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	Mean
Gs inorg tot (t)	962	196	307	561	74.9	69.7	109.6	79.4	3119	13199	2123	94.1	1728	565	1168	1623.7
Gs org tot (t)	138.2	107.0	123.6	88.6	73.7	147.8	148.5	95	247.4	817	117.8	84.5	212.9	114	140.7	177.1
Gs org/Gs tot %	12.6	35.3	28.7	13.6	49.6	68.0	57.5	54.5	7.3	5.8	5.3	47.3	11.0	16.8	10.8	28.3
Q tot mill $\text{m}^3 \text{yr}^{-1}$	83.9	95.2	87.2	70.0	60.2	67.6	95.0	64.8	82.8	79.3	83.8	52.4	103.3	72.9	135	82.2
Max q ($\text{m}^3 \text{s}^{-1}$)	23.5	57.3	57.7	17.2	19.2	23.9	20.2	10.1	100.2	118.6	32.3	19.9	63.7	46	31	
Max c (mg l^{-1})	113.0	47.0	68.2	455.3	42.8	18.7	18.7	70.0	606.1	2023.8	626.4	65.3	212.7	51.1	111.7	
Mean c (mg l^{-1})	11.47	2.06	3.52	8.01	1.24	1.03	1.15	1.22	37.68	166.53	25.34	1.8	16.73	7.75	8.66	19.6
Mean grain mm										0.087	0.094	0.048	0.150	0.031	0.060	0.078

Table 2. Station Fossum bru, 1987–2001. Organic and inorganic total transport, % organic transport, total and maximum annual water discharge, maximum and mean annual concentration, and mean annual grain size of suspended sediments

Year	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	Mean
Gs inorg tot (t)	1607.6	1473	3346.6	574.2	2199.1	1230.2	674	60651.4	1557.2	1246.2	2001.2	13102.3	2046	2391	6721.4
Gs org tot (t)	534	772.6	1116.8	469	904.5	1078.6	600.5	3337.1	589.1	574.7	775.6	1160	783	900.5	971.1
Gs org/Gs tot %	24.9	34.4	25.0	45.0	29.1	46.7	47.1	5.2	27.4	31.6	27.9	8.1	27.7	27.4	29.1
Q tot mill $\text{m}^3 \text{yr}^{-1}$	395.4	478.4	610.5	366.8	446.9	715.5	421.6	632.8	423.3	411.4	493.3	574.1	594.2	705.5	519.3
Max q ($\text{m}^3 \text{s}^{-1}$)	142.7	115.8	184.6	120.5	156	248.6	87.6	628.7	131.3	111.3	111.3	225.3	221	131	
Max c (mg l^{-1})	28.2	62.0	42.2	41.1	76.5	16.0	14.7	903.9	114.3	31.0	39.1	897.2	33.1	68.5	
Mean c (mg l^{-1})	4.07	3.08	5.48	1.57	4.92	1.72	1.6	95.84	3.68	3.03	4.06	22.82	3.44	3.39	11.3
Mean grain mm									0.081	0.039	0.017	0.020	0.025	0.021	0.034

variation is most probably due to changes in the extent of deposits exposed to erosion at different times of the year.

The organic fraction of the suspended sediment is defined by sample loss on ignition. Viewed from an ecosystem perspective, particulate organic matter (POM) concentration and export are significant characteristics of streams. The transport of organic material constitutes a trophic link between upstream and downstream communities, creating an integrated ecosystem (Golladay 1997). At Lia Bridge concentrations of POM remained below 5 mg l^{-1} for a large part of the season (Fig. 6), and are not correlated with water discharge. Values occasionally exceeded $5\text{--}10 \text{ mg l}^{-1}$, but these events seem to occur spontaneously, unrelated to water discharge. Except for the year 1996, with the extreme flood, the annual mean concentrations vary between 1 and 3.0 mg l^{-1} . The total annual POM transport was 817 t in 1996 and ranged from 73.7 t to 247.0 t during the other years. Thus, the year to year variations are not as large as for the transport of inorganic sediments. The mean total POM transport for all the years of measurement is 177.1 t. This amounts to 9.8% of the total transport of organic and inorganic sediments combined.

Sediment sources in upper Atna

A study of the source areas revealed that changes in sediment availability are important determinants of the pattern of variability. The most active sediment sources at present are situated in the tributary Vidjedalsbekken. Along a reach at 1000–1150 m a.s.l. (i.e. above the tree limit) this stream is undercutting the slopes of thick glacifluvial deposits, inducing mass movement (Fig. 7). A floodplain with a number of branching channels has developed. In the infrared air photo in Figure 8, the vegetation has a dark colour. The glacifluvial terraces appear grey as they are only sparsely vegetated. Areas of active erosion show as white patches where the vegetation has been destroyed. In the area A, the river is actively undercutting the adjacent slope. In the area B, the river channel is moving away from the edge of the deposit, causing a decrease in the mass movement activity, and a regeneration of the vegetation.

In the area C, the white and grey patches along the river channel indicate areas of active erosion and sedimentation along the river channel. Palaeochannels from the downwasting of the ice sheet are clearly visible in these areas. Cross-sections of the floodplain are

shown in Figure 9, indicating a width varying between 50 and 100 m along the 2100 m long reach. The longitudinal slope is relatively steep, with a mean of 0.006 m/m . Thus, the capacity and competence of the river is sufficient to transport the cobbles and boulders delivered from erosion of the lateral slopes. Upstream from the sections shown in Figure 9, there are several systems of the same type that deliver sediment to the river.

The large sediment input renders the channel system unstable, causing continuous shifting. The complicated pattern of short term and long term variations in suspended sediment concentrations and load may be explained in terms of channel changes and exposure to erosion. During large floods the coarsest fractions – cobbles and boulders – are mobilized. Some of the bed load is derived from frost shattering of bedrock in the high-lying part of the catchment, but most of it is derived from erosion of the sedimentary deposits. As the river undercuts an adjacent slope, mass movement may be triggered. When a large amount of material is plunged into the channel, the transport capacity will easily be exceeded and channel changes may occur.

Channel changes may also occur as a result of very large sediment supply from upstream sources. During periods of low and moderate discharges, the fine fractions will be washed away from the riverbed. The channel changes thus explain the shift between periods of high and low sediment yield. The floods have a double effect. First, the sediment load is increased due to heavy erosion during the flood. Secondly, the changes in the system caused by the flood increase the availability of sediment in the subsequent period. A major flood following another, like the one in 1996, may have access to more mobile sediments than the preceding one. The sediment yield is thus not entirely a result of random processes, but is to some extent controlled by the preceding history.

Particulate organic matter is predominantly derived from the present day vegetation of grass, moss and bushes. Very little is reworked from the glacifluvial deposits as they were deposited during a time of very little vegetation. The large transport in 1996 is attributed to the rainflood flushing out organic matter which had accumulated on valley slopes beyond the reach of high water during normal floods.

Sediment transport in Lower Atna

The concentration of suspended inorganic sediments for selected years at Fossum Bridge is presented in

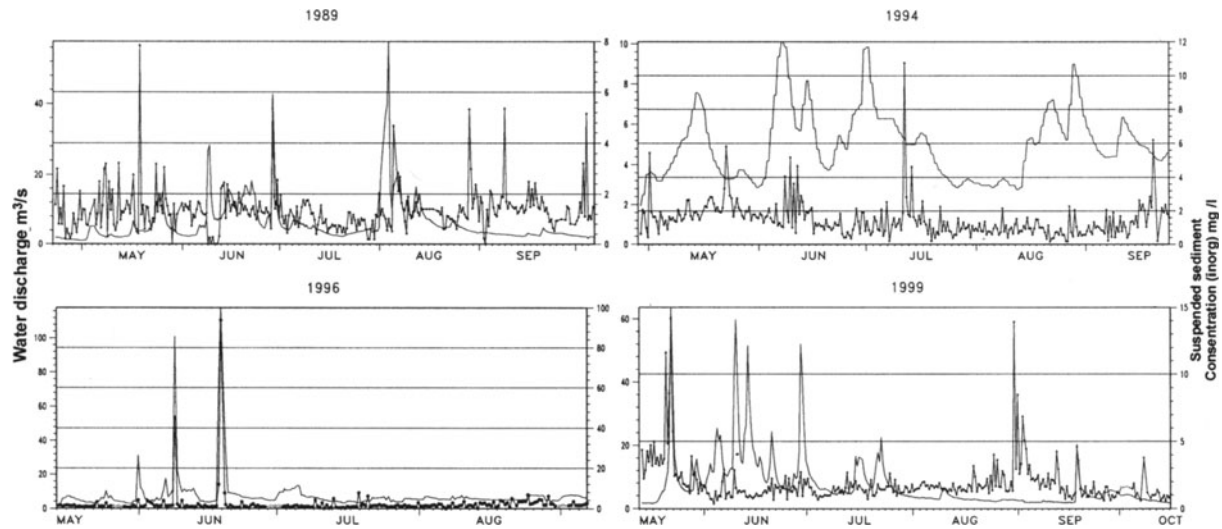


Figure 6. Suspended organic sediment concentrations (.....) and water discharge (—) at station Lia bru in upper Atna, in selected years.



Figure 7. Undercutting of adjacent slopes in the stream Vidjedalsbekken near cross-section P3 in Figure 9.

Figure 10. Concentrations are generally highest during the rising stage of a flood. During the first snowmelt flood in May 1990, the water discharge culminated at $184.6 \text{ m}^3 \text{ s}^{-1}$ on 4 May at 0700 hrs, whereas the particle concentration had already peaked at 32.3 mg l^{-1} on 2 May and had fallen to 23 mg l^{-1} during maximum water discharge. The same pattern was repeated during the rainflood in June. Rises in water discharge of the order of approx. $60 \text{ m}^3 \text{ s}^{-1}$ were not accompanied by any change in particle concentration. During the snowmelt flood in May 1992 there was also an increase in particle concentration to 27.8 mg l^{-1} during rising stage. A higher concen-

tration of 60 mg l^{-1} occurred at the culmination at $156.0 \text{ m}^3 \text{ s}^{-1}$ of the second part of the flood. However, the maximum concentration of 76.5 mg l^{-1} was recorded during the falling stage, when discharge was $131.3 \text{ m}^3 \text{ s}^{-1}$ (Fig. 10). During the start of the extreme flood in 1995, the concentration was 34.7 mg l^{-1} at $127.6 \text{ m}^3 \text{ s}^{-1}$ on 27 May at 0700 hrs. A significantly larger rate of increase was observed once the water discharge exceeded $400 \text{ m}^3 \text{ s}^{-1}$. At 1900 hrs on 31 May, the concentration was 60.8 mg l^{-1} and discharge $403 \text{ m}^3 \text{ s}^{-1}$, but had increased 15-fold to reach a level of 902.3 mg l^{-1} during the flood culmination of $628.7 \text{ m}^3 \text{ s}^{-1}$ on 2 June at 1900 hrs.

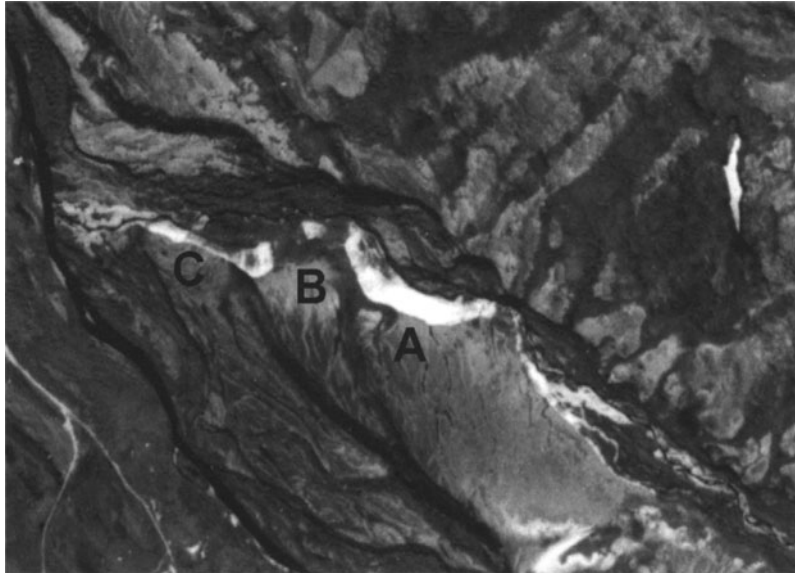


Figure 8. Aerial photograph of Vidjedalsbekken 1–4 km upstream from the main river. Downstream direction towards the upper left corner of the picture. A, B and C are referred to in the text. (Copyright Fjellanger Widerøe).

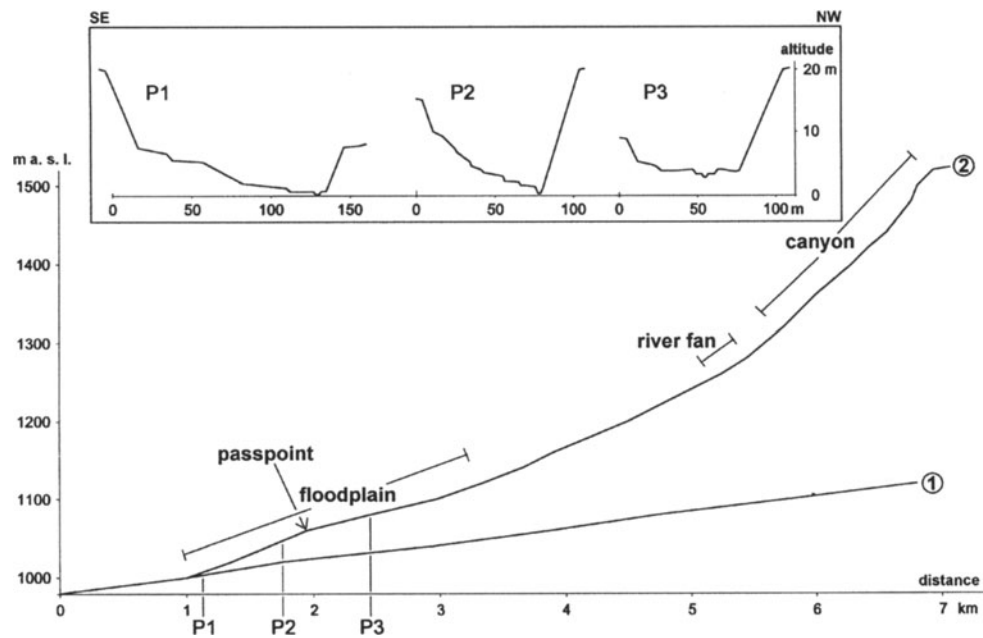


Figure 9. Slope of the main River Atna (1) and the tributary Vidjedalsbekken (2), and the profiles of the cross-sections P1, P2 and P3 in Vidjedalsbekken.

This pattern of increased concentrations during the falling stage of the flood (counter clockwise hysteresis) may be due to the high water level reaching new sediment sources when the discharge exceeds $400 \text{ m}^3 \text{ s}^{-1}$. The material thus eroded can then contribute to the high concentration levels during falling

stage. The pattern of high concentration during the rising stage of the flood (clockwise hysteresis) that was observed during the preceding years was attributed to erosion of sediments deposited in the river channel during earlier floods (Bogen, 1980). The rapid culmination of the concentration during mod-

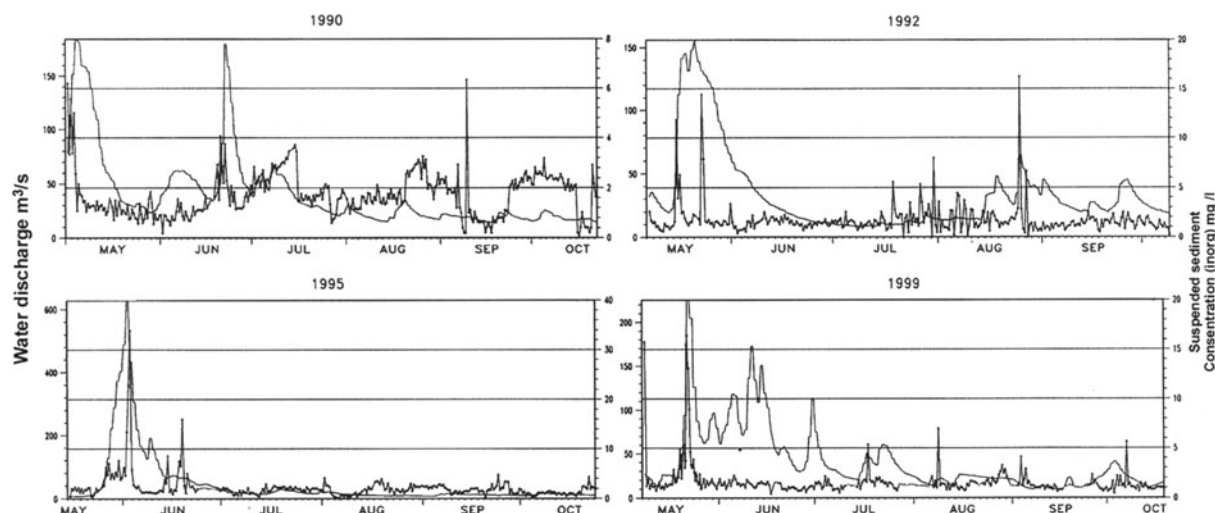


Figure 10. Suspended inorganic sediment concentrations (.....) and water discharge (—) at station Fossum bru in lower Atna, in selected years.

erate magnitude floods indicates that limited amounts of sediment are available for erosion. When a large flood has flushed the channels, another flood of comparable size is necessary to increase the concentration to any significant level. In 1999 a flood of $225 \text{ m}^3 \text{ s}^{-1}$ on 22 May was associated with an unusually high sediment concentration of 897.2 mg l^{-1} . The next flood culminating on 5 June at $118 \text{ m}^3 \text{ s}^{-1}$ gave 27.6 mg l^{-1} whereas the following one culminating 10 June had a maximum of just 6.5 mg l^{-1} during its rising stage. The $113 \text{ m}^3 \text{ s}^{-1}$ discharge peak on 30 June contained only 5.0 mg l^{-1} . The large concentration during the first flood was probably supplied by a slump during snowmelt in May, triggered by high soil moisture content. The sediments are then flushed away by successive floods.

The annual sediment yield at the lower station Fossum Bridge is shown in Figure 11 and Table 2. The mean over the years 1987–1994 was 1938 t. The calculated transport in 1995 was 60.651 t. Thus, the transport during this extreme food corresponds to more than 30 times the mean of the preceding years. There is apparently no major change in the sediment sources available at low and moderate water levels, as was the case in upper Atna. During the following year the annual transport returned to the pre-flood level. The slump that occurred in 1999 was most probably an isolated event. The annual mean of all the years of observation was 6721 t.

There was a poor correlation between suspended sediment concentration and water discharge (Fig. 12).

This probably reflects the low availability of erodible sediments in this catchment area of lower Atna. Loose deposits are unevenly distributed and the often dense forest cover protects them from erosion. The more favourable climate compared with the mountain area also causes faster regrowth on erosion scars.

The suspended sediments in lower Atna are much finer than the sediment in Upper Atna, and the seasonal variations are not as large. The content of sand (fractions less than 0.063 mm) varies from 2 to 20% and the amount of clay from 10 to 15%, Figure 13.

Similar to upper Atna, the highest concentrations of suspended particulate organic matter (POM) are associated with the floods. The maximum during the large flood in 1995 was 32 mg l^{-1} . During the flood of the other years the concentrations ranged up to a maximum of 17 mg l^{-1} . During low or moderate discharges the concentrations of POM are less than 5 mg l^{-1} (Fig. 14). The annual transport of POM ranged from 574 t in 1997 to a maximum of 3337 t in 1995.

The mean annual transport of POM during all the years of observation amounts to 971 t. This amounts to 12.6% of the total transport of organic and inorganic sediments. Both the total amount and per cent transport of POM is thus larger in lower Atna than in upper Atna. This is due to the larger contribution of POM from the forest vegetation in the low-lying areas compared to the alpine vegetation in the upper catchment.

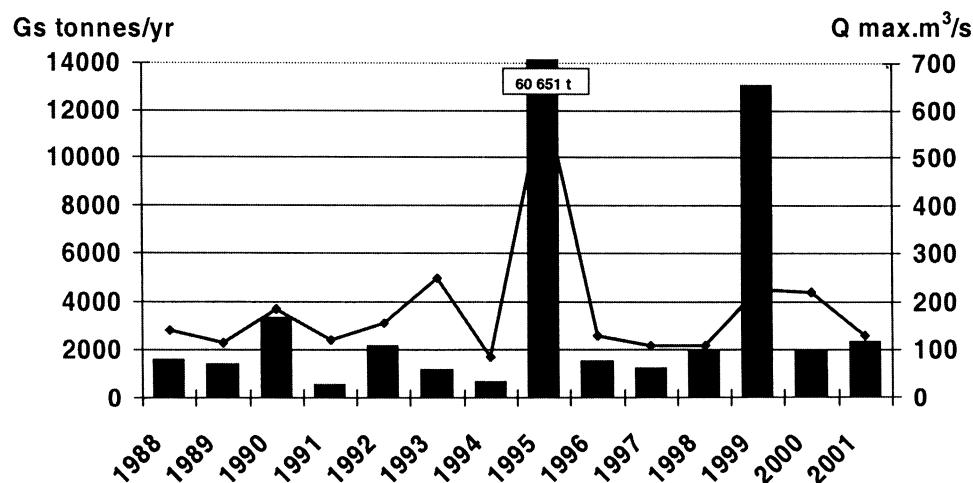


Figure 11. Annual suspended sediment transport (Gs, tonnes yr⁻¹; columns) and maximum annual water discharge (Qmax, m³ s⁻¹; lines) at Fossum bru.

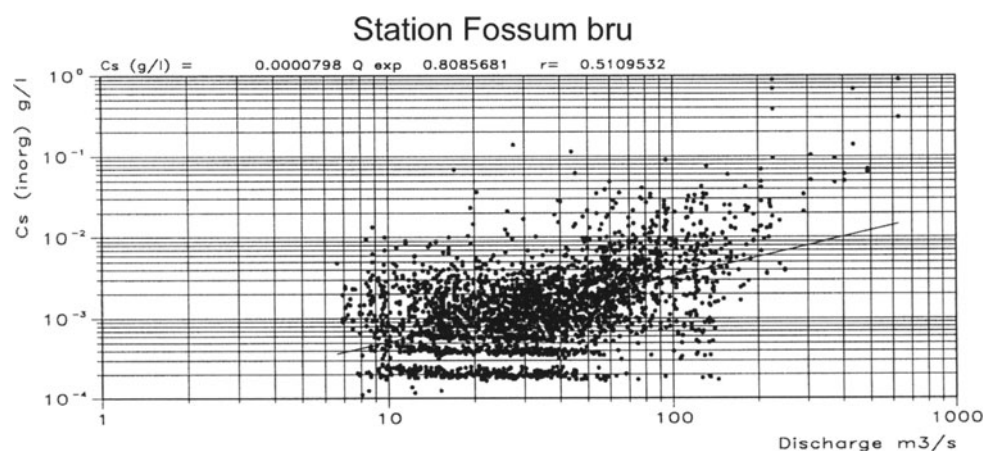


Figure 12. Regression analysis of suspended inorganic sediment concentration (C_s , g l⁻¹) vs. water discharge (Q , m³ s⁻¹), Fossum bru. The regression model is $C_s = 0.0000798 Q^{0.8085681}$, $r = 0.51$.

Sediment sources in lower Atna

Conditions along the lower Atna differ from those of upper Atna in that alluvial channel reaches exist upstream of the sediment monitoring station (see Fig. 1). These reaches are alluvial in the sense that the channel is formed by sediments supplied by the river. Alluvial reaches often have a regulating effect on the suspended transport rate in a river but in lower Atna the river bed material comprises cobbles and boulders and can not contribute suspended sediment. Sediments supplied from upstream sources may however settle on the low gradient alluvial reaches during low and moderate water discharges and may be re-suspended during higher water stages. This is probably the reason

why the correlation between discharge and sediment concentration is somewhat better in lower Atna.

Floodplain covered by fine overbank sediments does exist in a few areas. These overbank sediments are deposited during large water discharges above bankfull (i.e. recurrency interval much longer than 1.5–2 years). As the total supply of sediment during bankfull floods or lower is limited, there is little sediment accumulated on the river bed. During large magnitude floods of 100–200 years recurrency interval, like the one in 1995, the flow velocity across the floodplain may become very high and erode the overbank sediments. This is the reason why the sediment concentration during this major flood did not increase until the water discharge exceeded 400 m³ s⁻¹. Above

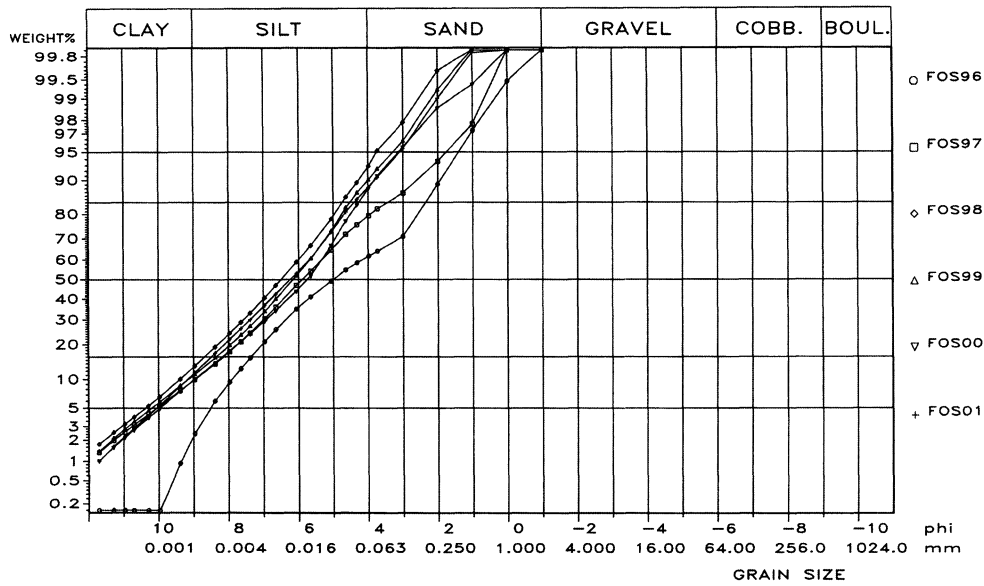


Figure 13. Mean annual grain size distribution of suspended sediment 1996–2001, Fossum bru. (Each curve represents the mean of all samples in one year).

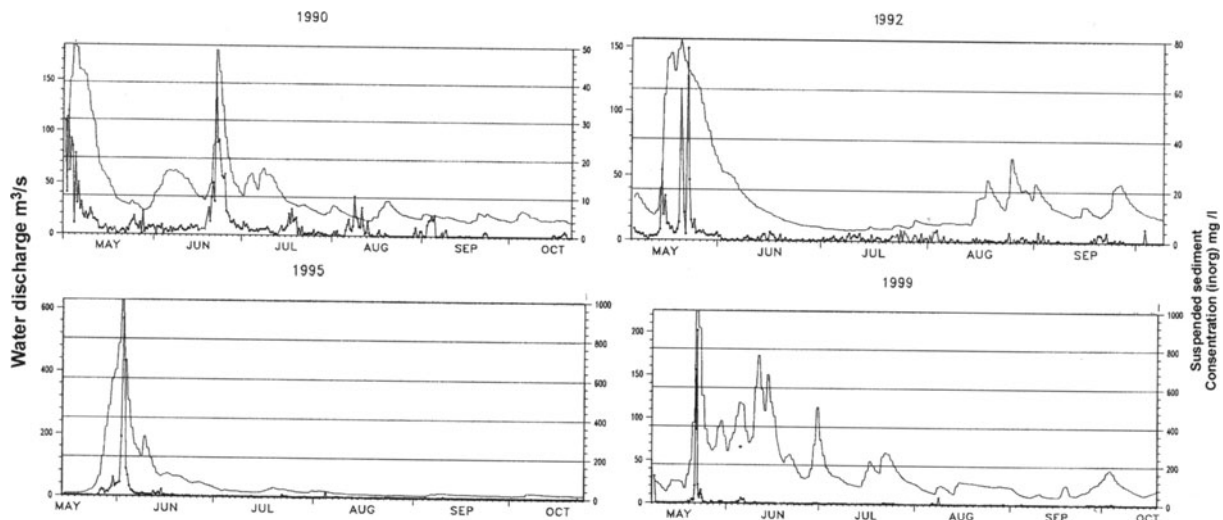


Figure 14. Suspended organic sediment concentrations (.....) and water discharge (—) at station Fossum bru in upper Atna, in selected years.

this level, the river may also undercut slopes of moraines and glaci-fluvial sediments that lie above the reach of fluvial erosion during lower water stages. The erosion by undercutting of slopes adjacent to the river channel is a widespread sediment source also in lower Atna. However, as the deposits are sparse and often situated away from the main channels, erosion of these deposits do not create a long-term change in sediment transport as in upper Atna. After the 1995 flood the sediment availability returned to normal. There were no large erosion scars created that might have

increased the susceptibility of sediments to erosion during low or medium water discharges.

Human activity contributes to increases in the sediment yield within the lower Atna. Runoff from cultivated fields in the area below lake Atnsjø is a significant source during particularly wet periods. This is determined as much by agricultural practice as by precipitation and snowmelt; actual volumes of resultant sediment flux vary somewhat from year to year. Landslides triggered by forest clearfelling on very steep slopes (Bogen 1986) occur only occasionally but may

deliver very large quantities of material into the river channel. This is well illustrated by the anomalously large sediment yield in 1999, (Fig. 11).

Conclusions

Measurements of sediment transport in two catchments within the Atna river basin during 14 years revealed large variations in suspended sediment transport. These occur on both short term (hours and days) and long term (year to year) scales.

There was almost no correlation between water discharge and suspended sediment concentration. This is attributed to the dominance of changes in the availability of erodible deposits, rather than hydrological factors, in determining the sediment supply.

Sediment is chiefly acquired by the river channel undercutting moraines and glasifluvial deposits. Exhaustion of sediment sources occurs as the face of the deposit is eroded back requiring ever higher water levels to achieve the same degree of erosion.

The pattern of long term sediment transport in upper Atna was found to be due to channel changes caused by major floods. These may bring the realigned channel into direct contact with newly erodible deposits allowing the impact of such floods to prevail for a long time. In lower Atna, floods do not generate channel changes to the same degree and the sediment supply is cut off as the flood level falls.

During periods when the river is not in contact with adjacent slopes, the sediment supply will be limited and the concentration of suspended sediments will remain low. In upper Atna the distance between the sediment sources and the monitoring station is short and the observed pattern of short-term variation in suspended sediment concentrations reflects more directly the erosional activity in the source area.

In lower Atna the alluvial reaches upstream from the monitoring station have a limited regulating effect on sediment flow and the correlation between water discharge and sediment concentration is slightly better than in upper Atna.

Acknowledgements

The sediment transport monitoring programme in the river Atna was initiated by the FORSKREF research

programme funded by the Norwegian Research Council. The continuation of the programme has been funded by NVE in co-operation with NINA, NIVA and SFT. Adrian Read is thanked for valuable comments to an earlier version of this paper.

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Fish distribution in a mountain area in south-eastern Norway: human introductions overrule natural immigration

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Key words: brown trout, Arctic charr, grayling, Siberian sculpin, European minnow, natural distribution, introductions

Abstract

The aim of this study is to examine the impact of man's interventions on the present day distribution of fish in a mountain area in southern Norway, the Atna river system. River Atna originates in the Rondane mountains at altitudes of nearly 1600 m a.s.l., and joins River Glomma at 300 m a.s.l. There are 98 lakes in the watercourse (701–1565 m a.s.l.). Lake Atnsjøen is the largest lake (5.0 km²). Data on the occurrence, origin and status of fish in lakes were obtained by means of interviews, questionnaires and written sources. Occurrence in rivers and streams was surveyed by electrofishing. While the lower reaches of River Glomma contain most of the freshwater fish species found in Norway, the Atna watercourse has a poor fish fauna. Physical conditions, e.g. steep river gradients and several impassable waterfalls have prevented fish from reaching most lakes and river stretches after the deglaciation some 6000 years ago. Five species of fish are regarded as native to the area; brown trout (*Salmo trutta*), Arctic charr (*Salvelinus alpinus*), grayling (*Thymallus thymallus*), Siberian sculpin (*Cottus poecilopus*) and European minnow (*Phoxinus phoxinus*). Although only native species are found in the area, the present distribution of these species within the watercourse is to a very large extent a result of human interventions during the past 100–130 years. Brown trout were originally found in the main branch of the river, including Lake Atnsjøen and a few small lakes ($n < 5$) further upstream, but it is now found in 65 lakes. Arctic charr were native only to Lake Atnsjøen, but now inhabit 20 lakes. Grayling remains restricted to River Atna below the waterfall at the outlet of Lake Atnsjøen. The natural distribution of Siberian sculpin is restricted to the main river below Liafossen waterfall (14 km above Lake Atnsjøen). During the 1890s, this species was accidentally introduced to Lake Setningsjøen, and subsequently spread to another three lakes further upstream. The European minnow was native only to the River Atna below Lake Atnsjøen, but was accidentally introduced to seven lakes in the course of this century. There are 24 fishless lakes in the watershed, mainly mountain lakes between 1033 and 1587 m a.s.l.

Introduction

The development of freshwater fish communities and their distribution in Fennoscandia is a result of historical and geographic processes (Huitfeldt-Kaas, 1918; Ekman, 1922). When Norway was deglaciated 10 000–6000 years ago, saltwater-tolerant fish species, including brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*), became established in inland waters along the western coast. During the Ancylus period some 8000–9500 years ago, the Baltic Sea was a

freshwater basin, and several fish species entered Norwegian inland waters from the south and east through Swedish watercourses. Brown trout and Arctic charr were also among these, and reached the upper reaches of the eastern rivers (Huitfeldt-Kaas, 1918). Later immigrants only reached lower altitudes, mainly due to land elevation. The immigration route from the south and southeast has been confirmed through DNA analysis of fish populations (Hindar et al., 1986; Refseth et al., 1998).

The Glomma River, which is the largest river system in Norway, in its lower parts contains 24 of the 30 native freshwater fish species found in the country (Hesthagen & Sandlund, 1996a; Økland & Økland, 1999). However, the number of species in the watercourse decreases with increasing altitude (Huitfeldt-Kaas, 1918; Svarte, 1983; cf. Figure 1). Steep gradients and impassable waterfalls were insurmountable topographical barriers for most species of fish. Large sub-alpine and alpine areas remained uncolonised or had a very poor fish fauna. As people settled into new areas, fish was introduced and translocated because it was an important food resource. The salmonids brown trout and Arctic charr were particularly attractive species (Huitfeldt-Kaas, 1918). A large number of Norwegian lakes have been stocked with these two species, in particular during the past 130–140 years (cf. Hesthagen & Sandlund, 1995; Rask et al. 2000; Vøllestad & Hesthagen, 2001). In addition, a large number of accidental introductions of freshwater fishes have occurred. This is especially the case with European minnow (*Phoxinus phoxinus*), which has commonly been used as live bait (Hesthagen & Sandlund, 1996b). Minnow may also be accidentally introduced when stocking with brown trout fry, and by migrating between watersheds through tunnels constructed for hydropower purposes.

Based on this, we may expect that the present fish communities in sub-alpine and alpine areas in southern Norway to a large extent are a result of human intervention. This was investigated in the Atna watercourse, which drains one of the highest-altitude areas within the Glomma watershed. The main objective of the study is to outline immigration routes, and to describe in detail the introduction and redistribution of freshwater fish within this watercourse, where fish has been considered an important source of food and recreation for centuries (Dahl, 1960).

Study area

The unregulated Atna watercourse originates in the Rondane mountains at altitudes between 1500–1600 m a. s. l., and the catchment area is 1323 km² (Fig. 2). River Atna joins River Glomma at an altitude of 308 m a.s.l. The Atna watercourse includes a total of 98 lakes larger than 0.011 km², with a total surface area of 11556 km² (Table 1). Only the largest lake, Lake Atnsjøen [4997 km², lake No 44 in Table 1] at 701 m a.s.l. is located on the main branch of the river. Two

larger rivers, Hira and Setninga, drain into River Atna below Lake Atnsjøen. River Setninga has a total of nine lakes [19–26 and 46 in Table 1]. There are three large waterfalls in the Atna watercourse; Solligarden in River Setninga, Atnbrufossen at the outlet of Lake Atnsjøen, and Liafossen about 14 km upstream of Lake Atnsjøen (Fig. 2). The waterfalls at both Solligarden and Liafossen are vertical barriers of several metres, and are impassable for any species of fish migrating upstream. On the other hand, Atnbrufossen waterfall has no vertical barrier, and may be passable for some species of fish.

The bodies of water that make up the Atna river system are only slightly affected by physical encroachments, farming or local pollution. However, some stretches of River Atna have been channelled, the river bed disrupted and its banks reinforced with stones and soil to prevent the river from flooding roads and agricultural land. River Atna is legally protected against hydropower development, and its upper reaches are within the Rondane National Park. The bedrock in most parts of the watershed consists of slowly weathering light sparagmite (Ofteidal, 1950; Holthedahl, 1953; Englund, 1973). The bedrock southeast of Lake Atnsjøen is dominated by granites and gneisses, making it somewhat more nutrient-rich than in the mountain areas. The Setninga area is dominated by dark phyllitic sparagmite which is also richer in nutrients. The quaternary geology is characterized by small amounts of deposits at high altitudes, and more deposits in the valleys (Gjessing, 1960). Impediment dominates in high mountain areas, with birch and various types of bush vegetation in sub-alpine regions, and pine forest in lower areas.

The climate in the Atna area is continental, with little precipitation and relatively cold winters (Nordli & Auen Grimnes, 2003). Near Lake Atnsjøen, the mean annual precipitation is 562 mm and air temperature is 0.8 °C (Bruun, 1957). Levels of acid components in the precipitation are low, with mean annual concentrations of SO₄-S, NO₃-N and NH₄-N of 0.40, 0.28 and 0.21 mg l⁻¹, respectively (Osen background station, 1988–97; Lükewille et al., 1998). Corresponding values for annual wet depositions of these compounds are 287, 186 and 149 mg m⁻², respectively. Localities in the uppermost part of the Atna watercourse, such as Verkilsdalsvatn [98], Langholvatn [93] and Bergedalstjern [84], are relatively acid and poor in nutrients, with pH and calcium contents of 5.02–5.57 and 0.16–0.27 mg l⁻¹, respectively (Aastorp, 1993). However, water quality improves in lower areas, and

Table 1. Lakes located in the Atna catchment area indicating altitude (m a.s.l.), surface area (size, km²), and occurrence of different species of fish: brown trout (BT), Arctic charr (AC), European minnow (EM), Siberian sculpin (SS) and rainbow trout (RT). Lakes devoid of fish are indicated as barren. For brown trout, the following symbols indicate: BT = self-sustaining, BT_S = stocked brown trout, (BT_S) = attempts to stock brown trout have failed, and (BT) = the occurrence of brown trout is uncertain, or the species occur in very low numbers. AC_L = lost stocks of Arctic charr, RT_L = introduced rainbow trout failed to become established. NN = the lake has no name on the official map.

No.	Lake	Altitude	Size	Species	No.	Lake	Altitude	Size	Species
1	Atnostjern	735	0.025	Barren	50	Gjermundtjern	805	0.014	BT
2	NN	735	0.042	Barren	51	Musvoltjern	892	0.042	BT
3	Hirsjøen, Lille	732	0.177	BT	52	Myldingtjern	896	0.025	BT, AC
4	Helaktjern	824	0.150	BT _S	53	Illmannstjern	1277	0.022	(BT), AC
5	Helaktjern	830	0.036	Barren (BT _S)	54	Illmannstjern	1277	0.054	(BT), AC
6	Reintjern	989	0.028	BT+BT _S	55	Illmannstjern	1279	0.015	(BT), AC
7	Hemtjern	894	0.034	BT+BT _S	56	Langbotn	1466	0.031	Barren
8	Grønfjelltjern	1189	0.021	Barren	57	Myrtjern	702	0.040	BT
9	Åsdalstjern, N	1132	0.280	BT _S	58	Svarttjern	702	0.040	BT
10	Åsdalstjern, Ø	1132	0.247	BT+BT _S	59	Blektjern	703	0.038	BT
11	Gråsjø	914	0.444	BT, AC, EM	60	Hesetjern	702	0.017	BT
12	Gråttjern	935	0.100	BT, AC, EM	61	NN	704	0.018	BT
13	Syrbekktjern	765	0.088	BT	62	Torsteintjern	704	0.070	BT
14	Skyvæltjern	1092	0.018	BT	63	NN	1236	0.062	Barren
15	Vintertjern	1062	0.028	BT	64	NN	1332	0.012	Barren
16	Steintjern	1135	0.037	BT, AC	65	Langbotntjern	1468	0.015	Barren
17	Storåstjern	1002	0.019	BT	66	Storbotn	1510	0.053	Barren
18	Storåstjern	1002	0.017	BT	67	Breitjern	706	0.060	BT
19	Setningsjøen	757	0.716	BT, AC, EM, SS	68	Reivtjern	708	0.022	BT
20	NN	760	0.017	Barren	69	Sætri	707	0.032	BT
21	Brennflytjern	1082	0.029	BT, RT _L	70	Sjogfonntjern	1033	0.018	Barren
22	Rundtjern	770	0.025	BT, AC, EM, SS	71	Rånåttjern	708	0.072	BT
23	Langtjern	771	0.112	BT, AC, EM, SS	72	NN	1299	0.016	Barren
24	Hamntjern	773	0.062	BT, AC, EM, SS	73	NN	1584	0.017	Barren
25	Vulutjern, S	1068	0.288	BT, AC	74	NN	1587	0.011	Barren
26	Vulutjern, N	1081	0.183	BT, AC	75	Midtbotntjern	1461	0.189	Barren
27	Stygbergertjern	874	0.024	BT, RT _L	76	Storoddtjern	709	0.027	BT
28	NN	748	0.019	BT	77	Svarttjern	767	0.020	BT
29	Åstjern	1016	0.020	BT	78	Skardtjern	1097	0.019	BT
30	NN	1166	0.016	BT	79	Motjern	751	0.011	BT
31	Aumskardtjern	1226	0.011	BT	80	Elgevatn	965	0.213	BT, AC _L
32	Aumskardtjern	1210	0.018	BT	81	Langtjern	894	0.062	BT
33	Aumskardtjern	1210	0.014	BT	82	Vidjedalsbotn	1536	0.011	Barren
34	Kvislåtjern	1241	0.199	BT, AC	83	Bergedalstjern, N	1232	0.044	BT _S
35	Stortjern	869	0.032	BT	84	Bergedalstjern, Ø	1233	0.065	BT _S
36	Småttjern	843	0.044	BT	85	NN	1467	0.089	Barren
37	Klettjern	910	0.019	BT	86	Skagsnebbtjern	1286	0.025	BT _S , AC
38	Finnsjøen	877	0.399	BT, C	87	NN	1534	0.019	Barren
39	Steintjern	1108	0.043	BT, AC _L , RT _L	88	NN	1534	0.021	Barren
40	Steintjern	1100	0.026	BT, AC _L , RT _L	89	NN	1565	0.020	Barren
41	Steintjern	1116	0.052	BT, AC _L , RT _L	90	NN	1565	0.021	Barren
42	Piktjern	1083	0.032	BT, AC _L	91	Dørålvatn	1266	0.112	BT
43	NN	976	0.020	BT	92	NN	1343	0.015	Barren
44	Atnsjøen	701	4.997	BT, AC, SS, EM	93	Langholvatn	1450	0.078	Barren
45	Kamptjern	1169	0.034	BT	94	NN	1550	0.047	Barren
46	Motjern	858	0.015	BT, AC	95	NN	1442	0.019	Barren
47	Vorddalstjern	860	0.074	BT, AC	96	NN	1502	0.032	Barren
48	NN	860	0.020	BT, AC	97	NN	1506	0.090	Barren
49	Laugartjern	860	0.022	BT, AC	98	Verkildalsvatn	1446	0.140	Barren

pH and calcium in the main river and in Lake Atnsjøen usually range between 6.0–6.5 and 0.5–1.0 mg l⁻¹, respectively (Blakar et al., 1997). The pH may fall to lower values during periods of high water flow, particularly during the spring snow melt.

Five species of fish are found in the Atna watercourse; Arctic charr, brown trout, grayling (*Thymallus thymallus*), Siberian sculpin (*Cottus poecilopus*) and European minnow. All populations of Arctic charr seem to be lake-spawners except one entirely stream-dwelling form in the stream Hornflågbekken which drains into Lake Vultjern [25 and 26] (Ola Hegge, pers. comm.). In the early years of the 20th century it was also reported that part of the Arctic charr population in Lake Atnsjøen migrated into River Atna to spawn (Helland, 1902). In the late 1970s, a few Arctic charr were caught in the outlet of the small tarn, Lake Myrtjern [57] about 150 m upstream of Lake Atnsjøen (Ryan, 1979). However, these were probably individuals that had migrated to feed in this tarn.

Some brown trout in Lake Atnsjøen become piscivorous (Parman 1987). These individuals may attain weights of 3–6 kg, and specimens of at least 8 kg have been caught (Rosseland, 1947). Their prey is mainly smaller Arctic charr in the pelagic zone, and probably also Siberian sculpin in the epibenthic zone. Growth analysis of brown trout shows that piscivory occurs from lengths of 23–30 cm (Kildal, 1981; Hesthagen unpubl. data). Larger brown trout of the River Glomma population migrate into River Atna to spawn (Linløkken, 1993). There are some exchange of brown trout between some of the small lakes, or tarns, close to the main river above Lake Atnsjøen and River Atna (cf. Fig. 2, Ryan, 1979). At least some of these lakes are very shallow, and probably freeze to the bottom during winter. Thus, the fish leave these lakes during autumn and return the following spring to feed.

In Lake Setningsjøen, a small proportion (<5%) of the brown trout differs by having a fine spotted pattern, and is genetically unique (Skaala et al., 1991; Skaala, 1992). The origin of the fine-spotted brown trout is unknown. There are only a few similar brown trout populations in Norway, at the Hardangervidda mountain plateau (southwestern Norway; Skaala & Jørstad, 1987).

Rainbow trout (*Onchorhynchus mykiss*) have been introduced into several lakes in the Atna watershed, but no self-sustaining populations have been established (cf. Table 1). Whitefish (*Coregonus lavaretus*) were stocked in the Åsdalstjerna lakes [9 and 10]

in 1897, but it did not become established (Helland, 1913).

Methods

The list of lakes in the Atna watershed (Table 1), including data on altitude and size, is based on the Regine database at the Norwegian Water and Energy Directorate (NVE), and was obtained by enumerating automatically all lakes larger than about 0.011 km² from 1:250,000 topographic maps (Norwegian Mapping Authority, Series 1501) (cf. Geir Taugbøl, NVE). Questionnaires and interviews were used to obtain data on fish populations in lakes (Hesthagen et al., 1993). This includes information on the occurrence of fish species, present population status characterised as 'unaffected', 'damaged' or 'lost', spawning facilities, stocking, and time of introduction. This information was obtained from a large number of persons who know the local fish resources well. Data on introductions were also obtained from various written sources. The occurrence of stream-dwelling species of fish in various parts of the Atna watercourse was assessed by electrofishing.

Results and discussion

A total of 24 lakes (24%) within the Atna watershed are barren of fish. These are mountain lakes located at altitudes between 1033 and 1587 m a.s.l. except for one very small lake at 735 m a. s. l. (Table 1). Brown trout were also introduced into several of these lakes during recent decades, but gillnet fishing by local fishermen have yielded no catch (game wardens Jan Hage-land, Norman Heitkøtter, Erik Winther, pers. comm.). The main reason is probably that these lakes are very shallow causing bottom freezing or oxygen deficiency during winter. There are also poor spawning facilities. However, acidification may also be a factor since low pH values, between 4.6 and 5.0, have been recorded in some lakes in the Rondane mountains.

The present distribution of freshwater fish species in the Atna catchment is to a large extent a result of human introductions, either planned or accidental. This is especially the case for brown trout, which is the most common fish species in the watercourse. There are a total of 60 lakes with self-sustaining populations of brown trout, and in addition populations maintained by stocking are found in 5 lakes (Table 1, Fig. 2).

Brown trout is probably native only to the main branch of the river system, extending upstream to Liafossen waterfall, and probably to a few small lakes or tarns close to the main river. Brown trout can easily ascend the Atnbrufossen waterfall at the outlet of Lake Atnsjøen (cf. Fig. 2, Anton Brænd, pers. comm.), and it may also have invaded Lake Atnsjøen from the formerly glacier-dammed Lake Øvre Glomsjø (see further discussion on the immigration of Arctic charr). Written historical records show that brown trout have been introduced in localities in the area from the 1700s almost up to the present. Since the introduction of brown trout into Lake Elgevatn [80] around 1940, the species occurs in the river above Liafossen waterfall. It is unlikely that brown trout are native to Lake Setningsjøen [19] because of the impassable waterfall at Solligarden.

Arctic charr are also commonly occurring in the Atna watercourse, and are presently found in 20 lakes (Table 1, Fig. 2). Most populations were probably introduced, but Arctic charr are probably native to Lake Atnsjøen, and it was known to occur in some lakes in the area in the late 1700s (Hiorthøy, 1785). Only some of the introductions during the late 1800s can be documented, e.g., in the Vulutjerna lakes [25 & 26], Elgevatn [80] and Finnsjøen [38]. Arctic charr are probably not able to ascend the Atnbrufossen waterfall. This renders immigration from the southeast improbable, if not impossible. Huitfeldt-Kaas (1918) mapped the distribution of Arctic charr within the Glomma watershed and suggested that the species might have invaded Lake Atnsjøen from the formerly glacier-dammed Lake Øvre Glomsjø, which was situated north of present day Lake Atnsjøen. This lake was created some 6000 years ago at an altitude of 720 m a.s.l. (Lake Atnsjøen is at 701 m a.s.l.). Huitfeldt-Kaas (1918) also suggested that this might explain the present-day apparently natural occurrence of Arctic charr in other lakes in the upper reaches of the Glomma watercourse, such as Savalen and Aursunden (cf. Fig. 1). Lake Savalen only supports brown trout and Arctic charr, while Lake Aursunden also contains other species, both native and introduced.

Genetic analysis of Arctic char from Lake Atnsjøen showed allele frequencies similar to that of populations in south-eastern Norway, and a low level of genetic variability (cf. Hindar et al., 1986; K. Hindar, pers. comm.). These results are consistent with both natural immigration and introduction of Arctic charr from the same region by humans. Thus, no final conclusion can be drawn based on genetics.

Arctic charr did occur in Lake Atnsjøen in the early 1800s (Søndre Gudbrandsdalens Sørenskriveri, 1910; Hiorthøy, 1785). The technique of artificial rearing was not known in Norway until the late 1800s (cf. Bleken Rud, 1967). Because Lake Atnsjøen is distant from other lakes that contained Arctic charr in the early 1800s, an early introduction of Arctic charr into Lake Atnsjøen must have involved transport of live fish over long distances. This does not seem likely, and we therefore conclude that Arctic charr most probably are native to Lake Atnsjøen.

In Lake Setningsjøen, however, Arctic charr has most certainly been introduced. The lake could not be invaded from the south due to the barrier at Solligarden waterfall. It is also unlikely that Lake Setningsjøen, at 757 m a.s.l., received Arctic charr from Lake Øvre Glomsjø, which was situated at 720 m a.s.l.

There are at least two major reasons for a high number of introductions of Arctic charr and brown trout during the late 1800s. First, the Norwegian Parliament in 1870 adopted a law enabling private persons to lease fishless lakes on state lands. Secondly, the technique of artificial propagation was introduced (Huitfeldt-Kaas, 1918). In the 1870s, the Åsdalstjerna lakes [9 & 10] were leased by the professors Halvor Heyerdahl Rasch and Jens Andreas Friis who set about to release small brown trout caught by angling in downstream areas (Friis, 1971). It appears, however, that this introduction failed. When the lakes were leased by another person in 1897, they were still considered fishless (Helland, 1913). When the brown trout populations became established around 1900, the techniques for artificial rearing were well established. This facilitated introduction of reared juvenile fish rather than having to catch, transport and release wild specimens. During the late 1800s, a large number of small hatcheries were established throughout the country (Bleken Rud, 1967). At Sollia, close to Lake Atnsjøen, a hatchery was established in 1886, producing both brown trout and Arctic charr fry (Inspector of Fisheries, 1890). The fry was probably stocked mainly in nearby lakes. When the lakes S. and N. Vulutjern [25 and 26], situated in Fron municipality, were stocked with Arctic charr fry in 1870s (Sunde, 1936), the fish probably derived from a hatchery in Fron.

Grayling has a very limited distribution in the Atna watercourse, being restricted to River Atna below Atnbrufossen. Mature grayling from River Glomma ascend River Atna to spawn in May, reaching the stretches below Atnbrufossen in late June (Helland, 1902). Most grayling descend the river in late autumn,

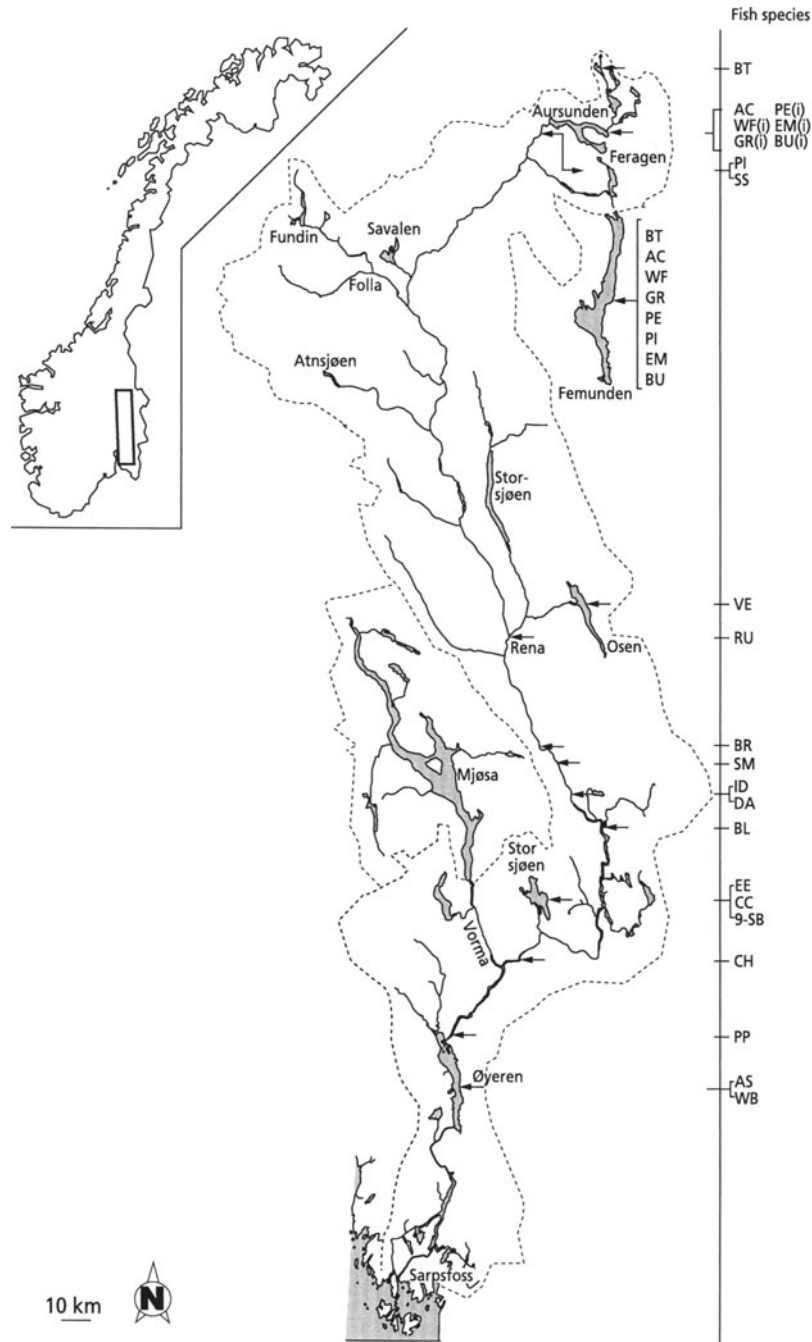


Figure 1. Outline map of the eastern part of Glomma watershed, showing locations of the largest rivers and lakes and indications of the upper limit of occurrence for different freshwater species of fish. The species of fish are: AC = Arctic charr, AS = asp (*Aspius aspius*), BL = bleak (*Alburnus alburnus*), BR = bream (*Abramis brama*), BT = brown trout, BU = burbot (*Lota lota*), CC = crucian carp (*Carassius carassius*), CH = chub (*Leuciscus cephalus*), EE = eel (*Anguilla anguilla*), EM = European minnow, GR = Grayling, PE = Perch, PI = pike (*Esox lucius*), RU = ruffe (*Gymnocephalus cernuus*), SS = Siberian sculpin, VE = vendace (*Coregonus albula*), WB = white bream (*Blicca bjoerkna*), WF = European whitefish, SM = smelt (*Osmerus eperlanus*), ID = ide (*Leuciscus idus*), DA = dace (*Leuciscus leuciscus*), 9-SB = nine-spined stickleback (*Pungitius pungitius*), PP = pikeperch (*Stizostedion lucioperca*). i = introduced species. Redrawn from Svarte (1983). The location of Lake Femunden, which is situated outside of the Glomma watershed, is also shown. Six different species were introduced to the upper parts of Glomma catchment when a channel was built between Lake Femunden and Lake Feragen in the River Glomma catchment in 1762 (Huitfeldt-Kaas, 1918).

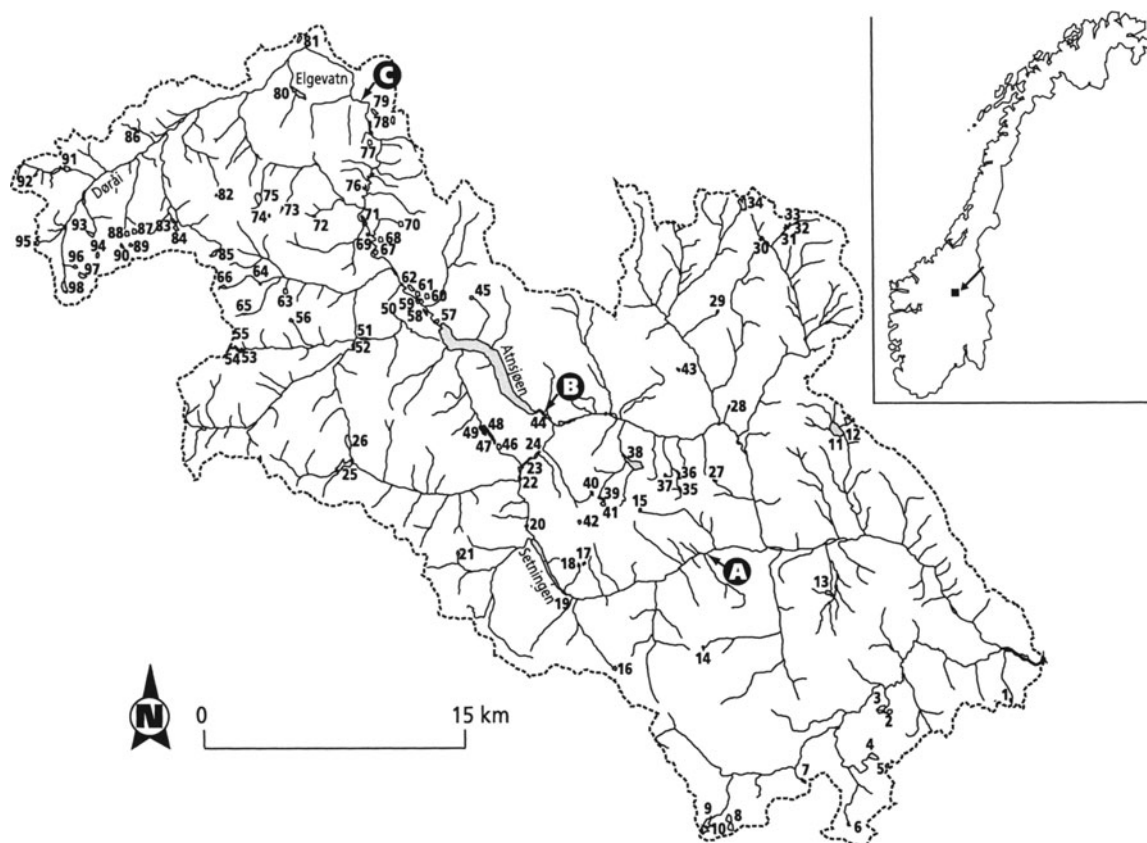


Figure 2. Outline of Atna watershed showing the geographical location of the study lakes as indicated by numbers (cf. Table 1). The locations of waterfalls are indicated by arrows: Solligarden (A), Atnbrufossen (B) and Liafossen (C).

but some specimens may stay the winter in a small lake just below Atnbrufossen. The only known attempt to introduce grayling further upstream was in 1940 when two adult fish were caught in the river and released in Lake Atnsjøen near its outlet. However, both individuals were soon recaptured in gill-nets (Syver Moen, pers. comm.). Grayling is considered a less valuable food resource than brown trout and Arctic charr, and has rarely been translocated in Norwegian rivers.

The abundance of grayling in River Atna has apparently decreased significantly during recent decades (Anton Brænd, pers. comm.). This is supported by electrofishing surveys in the river, yielding very few juvenile fish (Hesthagen et al., 2004). A similar reduction in the abundance of grayling has been observed in the River Glomma (Linløkken, 1995). Originally, grayling appeared to migrate over long distances for spawning and feeding in River Glomma (Andersen, 1968), but the construction of a number of hydroelectric dams between 1971 and 1984 apparently affected these migrations (Linløkken, 1993).

The natural distribution of Siberian sculpin in the Atna watercourse probably extended as far as Liafossen waterfall in the main river. The species occur in high densities throughout the river (Hesthagen et al., 2004), and is also relatively numerous in the epibenthic habitat of Lake Atnsjøen (Austigard & Holmedal, 1998). Siberian sculpin is also found in the River Setninga, as a result of an accidental introduction in the 1890s (Anton Brænd and Åsmund Wollum, pers. comm.). Local fishermen caught Siberian sculpin with beach seines in River Atna during autumn, to be used as bait on long-lines fishing for brown trout during winter. The fish were kept alive in enclosures in Lake Setningsjøen. After escaping from the enclosures, the Siberian sculpin spread into three lakes further upstream within a few years (Rundtjern, Langtjern and Hamntjern [22, 23 & 24], Fig. 1). Line fishing for brown trout in Lake Setningsjøen used to be an important source of income for several persons in that district (Åsmund Wollum, pers. comm.).

The natural distribution of Siberian sculpin up to Liafossen waterfall means that the species have been able to ascend Atnbrufossen waterfall below Lake Atnsjøen. Siberian sculpin is regarded as a bottom-dwelling species (cf. Andreasson, 1971), with a pronounced ability to move along the river substratum in spite of high water discharge rates. According to Nybelin (1969), the closely related species bullhead (*C. gobio*) has a positive rheotactic behaviour, i.e. they tend to migrate upstream until they encounter impassable barriers. After the accidental introduction of bullheads into the River Utsjoki in northern Finland, they dispersed 14.2 km upstream in the course of 15 years (Pihlaja et al., 1998). Siberian sculpin have a limited distribution in southern Norway, being mainly restricted to lower parts of River Glomma and tributaries (unpubl. data). Their limited distribution has been explained by the fact that this species, with a southerly or south-easterly invasion route, was one of the most recent immigrants in its group; the so-called 'Lake Mjøsa–Lake Storsjøen fishes' (Huitfeldt-Kaas, 1918). The fact that the species is absent west of the Glomma watercourse seems to confirm this. This also explains their limited distribution in mountain regions in northern parts of Scandinavia (Andreasson, 1972).

European minnow is indigenous to the Atna catchment only below Atnbrufossen. However, the species have been accidentally introduced to at least seven lakes in the watercourse during the 20th century. The first introductions in the area were into lakes Gråsjø and Gråttjern [11 & 12] in the southeastern part of the watershed, probably in the early 1900s (Asbjørn Dellerud, pers. comm.). The second introduction of European minnow was made into the northern part of Lake Atnsjøen in 1962 by anglers who had used the fish as bait (Anton Brænd, pers. comm.). The first specimens were observed near the outlet of the lake in the early 1970s. A few European minnows have also been caught in the inlet stream of Lake Torsteintjern [62], which is located a short distance upstream of Lake Atnsjøen (Ryan, 1979). However, it is not known whether this locality and other tarns in this area contain self-sustaining populations of the minnow. The latest recorded introduction of European minnow in the area occurred during the 1970s, when the first specimens were observed in the four lakes in the Setninga branch [19, 21–23]. However, European minnow are difficult to detect during the initial phase of establishment, and they may therefore have been introduced in more localities in the Atna watershed in recent years (cf. Hesthagen & Sandlund, 1996b).

The natural distribution of European minnow in Norway was limited to the south-eastern part of the country, and some river systems in central and northern Norway (Huitfeldt-Kaas, 1918). However, a considerable redistribution has taken place during this century, and the species is now found in most of southern Norway (Hesthagen & Sandlund, 1996b). European minnow are regarded as a threat to brown trout populations, particularly in localities with restricted spawning and nursery areas (Borgstrøm et al., 1996). However, the abundance of European minnow in lakes seems to be limited by both lake morphology and fish species composition, and the actual impact on brown trout is not very well documented (Taugbøl et al., 2002). The species is most abundant in shallow waters that contain only brown trout (cf. Hesthagen & Sandlund, 1996b). Lake Atnsjøen sustains a very sparse population of European minnow. The lake has a steep littoral zone inhabited by relatively dense populations of brown trout, Arctic charr and Siberian sculpins (Austigard & Holmedal, 1998; Saksgård & Hesthagen, 2004). On the other hand, the populations of European minnow in the shallower lakes in the Setninga area are regarded as relatively dense. In River Atna, virtually no European minnow have been caught during electrofishing surveys in recent years (Hesthagen et al., 2004). This is probably related to both physical conditions, with an unstable river bed and fast currents, and to interspecific competition from brown trout and Siberian sculpin (cf. Hesthagen et al., 2004).

The non-native rainbow trout has been introduced into several lakes in Atna during the past 70 years. The first introductions were in the lakes S. and N. Vulutjern [25 & 26] during the 1930s (Åsmund Vollum, pers. comm.). Some of these individuals were later captured in the downstream Lake Rundtjern [22]. Later, the species was introduced to Lake Styggbergertjern [27] and Lake Skyvæltjern [14] in the 1950s, and to lakes Steintjørnene [39, 40 & 41] in the 1970s. It disappeared from these lakes within a few years. The latest introduction of rainbow trout was made in the spring of 1985–1987 when one-year-old fish of 12–17 cm length were stocked in Lake Brennflytjern [21], Lake Kamptjern [45] and Lake Vorddalstjern [47] (Hans Bondal, pers. comm.). The following autumn, gill-net fishing in all these lakes caught a large proportion of the stocked fish. During the few summer months, the rainbow trout had reached weights of 250–300 g, and the largest fish was about 1/2 kg. However, no self-sustaining populations of rainbow trout have been

established in the Atna watercourse. This corresponds with the general experience from extensive stocking of this species in Norway for more than 100 years. Very few self-sustaining populations have been established, and Hindar et al. (1996) suggested that this may be due to the presence of parasites pathogenic to the early life stages of rainbow trout.

Several populations of brown trout and Arctic charr have declined and even disappeared since the 1930s. For instance, this is the case for Arctic charr both in Lake Gråsjø [11] and Lake Elgevatn [80] (Asbjørn Dellerud & Jørn Elgevasslien, pers. comm.). Some of the damage can be related to acidification, in particular in the upper reaches of the river system. In order to counteract the acidification process, liming with powdered limestone was performed repeatedly on Lake Elgevatn from the late 1980s up to 1997. The population of brown trout in this lake now seems to have recovered, and a yield of about 320 kg is reported each year (Jørn Elgevasslien, pers. comm.).

Several populations of Arctic charr in the lower reaches of the Atna watercourse have also disappeared. The sudden disappearance of Arctic charr in Lake Gråsjø [11] remains unexplained. The phenomenon has been blamed on heavy exploitation with gill-nets, but this seems improbable. The abundance of brown trout in the lake was unchanged, as were the populations of Arctic charr and brown trout in the neighbouring Lake Gråtjern [12]. The lake is not affected by local pollution. Acidification should also be disregarded as the water is nearly neutral (pH = 6.39) and has a low concentration of toxic inorganic aluminium ($7 \mu\text{g l}^{-1}$) (cf. Hesthagen & Sandlund, 1995). In the early 1990s, Lake Gråsjø was re-stocked with wild Arctic charr from a lake outside the Atna watershed, and the species is again reproducing in the lake.

Conclusion

More than 95% of the fish populations in the lakes in the Atna watercourse exist as a result of human intervention, mainly deliberate introductions due to the fact that fish have been considered as an important source of food. This is particularly the case for brown trout and Arctic charr. However, accidental introductions of European minnow and Siberian sculpin have also occurred, caused by the use of these species as live bait in recreational, subsistence and commercial fisheries.

Acknowledgements

We wish to thank Ola Hegge and Jostein Skurdal for valuable comments to earlier versions of this manuscript. Hans Bondal, Anton Brænd, Jørund Elgvasslien, Jan Hageland, Norman Heitkøtter, Syver Moen, Åsmund Wollum, Bjørn Wegge and Erik Winther provided valuable information on the occurrence, status and introductions of various species of fish in the Atna watercourse. Bjørn Olav Rosseland granted us access to the diaries of his father, Leif Rosseland, who worked with various fishery projects in the Atna area during the 1930s and 1940s. Leif Rosseland was for several years the scientific leader of the Fish Research Division of the Directorate for Wildlife and Freshwater Fish.

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ATNA RIVER



Periphyton in running waters – long-term studies of natural variation

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Key words: Periphyton, reference conditions, Norway, natural variation, species composition, species diversity

Abstract

The objective of this study in River Atna, Norway, was to analyse the spatial and temporal variation in species composition and diversity of the periphyton community in a pristine sub-alpine / boreal watercourse. The variations in the biotic parameters were related to selected environmental factors. We addressed epilithic algae and species living epiphytic on epilithic algae and submerged bryophytes. The sampling sites were located in the alpine, northern boreal, and mid boreal biomes. There was considerable spatial variation in species composition and diversity. This variation showed close correlation with natural gradients in water temperature and nutrient concentration. Three or four periphyton community categories could be distinguished in terms of species composition, diversity, and environmental variables. At high altitudes (1150–740 m a.s.l.) in cold water temperatures and extremely low nutrient contents, there was very low species diversity, only including algae known from ultra oligotrophic cold waters, e.g. *Scytonematopsis starmachii* (cyanobacteria) and *Klebsormidium rivulare* (green algae). The second category, at medium altitudes (701–522 m a.s.l.), was characterised by somewhat higher water temperatures and nutrient contents, and the species diversity was higher. This category included algae known from somewhat richer waters, e.g. *Stigonema mamillosum* (cyanobacteria) and *Zygnema spp.* (green algae). The third category was located at approx. 522 m a.s.l., had low water temperatures, relatively high alkalinity, and was characterised by *Tolypothrix distorta* (cyanobacteria) and *Ulothrix zonata* (green algae). A possible fourth category was found in the lower part of the river (350 m a.s.l.), where periphyton was distinguished by high diversity. At the individual sampling localities, species diversity showed strong seasonal variation, but otherwise high temporal stability. Over the 12 years of observations, there was only a weak temporal trend; towards species initially occurring only at low altitudes and high nutrient content. The combination of high temporal stability and high spatial variability, correlating closely with environmental gradients, is the main reason why periphyton observations have become an important constituent in water quality assessment.

Introduction

Few periphyton studies were conducted in Norway before such studies were initiated as part of regular monitoring programmes in 1978 (Knutzen et al., 1980; Lindstrøm, 2000). Since then, more than 900 running water localities have been surveyed. Most studies were restricted in time, lasting only one to two years, or they were conducted in rivers impacted by human activity. The studies in River Atna are the first long term observations in an unpolluted river. This scarcity of long term observations, particularly in running wa-

ters, appears to be the situation in many countries (Whitton et al., 1991; Stevenson et al., 1996; Prygiel et al., 1999). As a consequence, we know little about periphyton communities in unpolluted pristine rivers, and particularly little about temporal variation. Norway has a vast number of watercourses that display great variety in hydrology, climate and chemical conditions (Slevig, 1992). A good proportion of these rivers are still relatively unaffected by human impacts and may provide valuable basic knowledge on biological reference conditions. The implementation of the European Water Framework Directive, which

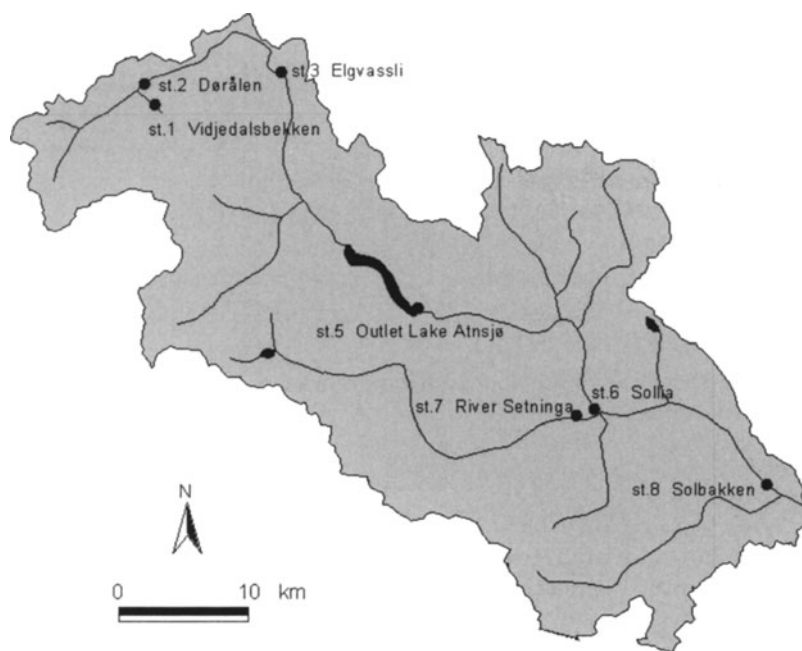


Figure 1. The Atna watercourse, in southeastern Norway, with stations (st. 1–8) for periphyton observations. Cf. Table 1.

requires periphyton observations to be a regular constituent of monitoring programmes, has actualised the demand for this type of knowledge (Wallin et al., 2002). Another reason to acquire knowledge on reference conditions in nutrient poor waters is the need to assess impacts of long range transboundary pollution and climate change, which seem to affect these waters in particular (Henriksen, 1999).

The objective of this study in River Atna, Norway, was to analyse the spatial and temporal variation in species composition and diversity of the periphyton community in a relatively pristine sub-alpine / boreal watercourse. The variations in the biotic parameters were related to selected environmental factors. We addressed epilithic algae and species living epiphytic on epilithic algae and submerged bryophytes. The focus is on community composition and taxonomy. Unfortunately, the reference value of modern periphyton studies is often reduced due to insufficient taxonomic information. Finally we report on the related development of reliable and replicable methods that can be applied in the physically demanding and variable environments of alpine and sub-alpine running waters.

Study area

The Atna watercourse is located in south-eastern Norway. It exhibits a wide range of physical, climatic and chemical conditions. The sources are at 1200 to 2000 m a.s.l. in the Rondane Mountains, and River Atna joins River Glomma at 320 m a. s. l. (Fig. 1). The catchment is little affected by human activity (approx. 450 inhabitants in a total area of 1323 km²), and fairly unaffected by the airborne pollution that impoverishes a substantial number of the watercourses in southern Norway (SFT, 1998). The bedrock, mainly sparagmite, is inert and nutrient poor, and contributes little electrolytes and nutrients to the water (Bogen, 2003). The soil cover increases with decreasing altitude, but is generally thin.

We sampled periphyton at seven stations, five in the main watercourse and two in tributaries (Table 1). According to Moen (1998), the stations comprise three biomes: (A-C1) alpine – mildly continental, (Nb-C1) northern boreal – mildly continental, and (Mb-OC) mid boreal – continental to oceanic. The theoretical growth period (days with average air temperature above 5 °C) increases from less than 110 at the upper st.1 Vidjedalsbekken (1150 m a. s. l.) to almost 150 at the lower st.8 Solbakken (380 m a. s. l.). Climatic conditions are described by Nordli & Grimenes (2004). The days are long, at least 18 hours during

Table 1. Localities for periphyton observations (station 1-8), River Atna, Norway. The biome definitions are as follows (Moen, 1998): *A-CI*: Alpine – mildly continental (400–500 mm annual precipitation), *Nb-CI*: Northern boreal – mildly continental (400–500 mm annual precipitation), *Mb-OC*: Mid boreal – continental to oceanic (500–700 mm annual precipitation). Days in growth period (Moen, 1998): average temperature > 5 °C. *: At average discharge current velocity differs with distance from the riverbank, in a moderate (20–70 cm s⁻¹), swift (50–100) and very swift (80–120) zone.

Station	Name	X and Y co-ordinates ED-50	Altitude (m a.s.l.)	River width (m)	Current velocity at average discharge (cm s ⁻¹)	Inso- lation	Biome	Days in growth period
1	Tributary - Vidjedalsbekken	32V 5432 68723	1150	2	30–75	Good	A-CI	<110
2	Dørålen	32V 5422 68738	1020	5–10	60–150	Good	A-CI	+/-110
3	Elgvassli	32V 5530 69758	740	10–12	30–100	Good	Nb-CI	110–120
5	Outlet Lake Atnsjøen	32V 5645 68586	701	40	Rapid*	Good	Nb-CI	110–120
6	Sollia	32V 5787 68518	522	25	40–150	Good	Mb-OC	130–140
7	Tributary- Setninga (before 94: 5787 68515)	32V 5774 68516	525	15	50–150	Good	Mb-OC	130–140
8	Solbakken	32V 5923 68473	380	50	30–150	Good	Mb-OC	140–150

the summer growth season. The river width increases from 3 m to approximately 50 m. There are no canopy trees that shadow at any station, and all sampling stations have sufficient insolation to allow proper primary production.

The average annual discharge at the outlet of Lake Atnsjøen is 10.32 m³ s⁻¹ (Tvede, 2004). River Atna is unregulated and exhibits rapid changes in water flow. Consequently, the riverbed may at times be quite unstable and spates occur regularly. The highest floods with the sharpest peaks are during snow melt and in early summer, when rainstorms may combine with remnants of frost in the soil and cause quick runoff (Fig. 2). Average annual discharge at the outlet in the river Glomma is 28.5 m³ s⁻¹.

All sampling stations are located in riffles and have high current velocity (Table 1). For example, average current velocity 2 cm above the substratum was 65 cm s⁻¹ in two transects at st.3 Elgvassli when discharge at st.5 Outlet Lake Atnsjø was 10 m³ s⁻¹. It has proved to be physically difficult to sample periphyton properly when discharges at the outlet of Lake Atnsjøen are above 25 m³ s⁻¹.

The substratum grain size (median diameter) in transects used for periphyton observation is shown in Table 1. Large (20–40 cm) and small (2–20 cm) stones comprised 63% to 90% of the substratum in all transects. The coarse substratum reflects the high current

velocity and the demanding flow regime. Total disruption of the substratum during spates is prevented by blocks (median diameter >40 cm) at most stations. The transport of fine sediment varies and increases with activation of glacialfluvial deposits in the upper part of the watershed (Bogen, 2004). The activation is episodic and mainly caused by major floods, e.g., June 1995 (Fig. 2.)

The watercourse Atna is generally nutrient poor, has low conductivity and low humic content (Table 2). The water is extremely low in dissolved solids in the upper reaches (i.e. st.1 Vidjedalsbekken and st.2 Dørålen). Increasing soil cover and vegetation contribute to slightly increased nutrient content in the lower reaches. TOC (total organic carbon) increases from 0.5 mg l⁻¹ at the two upper stations to around 1.3 mg l⁻¹ at st.8 Solbakken. A similar increase along the river seems to take place in tot-P (total phosphorous). The water has low content of calcium and other basic cations, and is vulnerable to acidification. This is counteracted locally by the inflow of groundwater and by tributaries that drain somewhat richer bedrock than the insoluble sparagmite in the main river, e.g. st.7 River Setninga (Table 2). The concentration of calcium, which is only 0.5 mg l⁻¹ in the upper reaches (stations 1 and 2), increases to 1.7 mg l⁻¹ at the lower station in the main river, st.8 Solbakken. Most of this increase occurs after the confluence with the tribu-

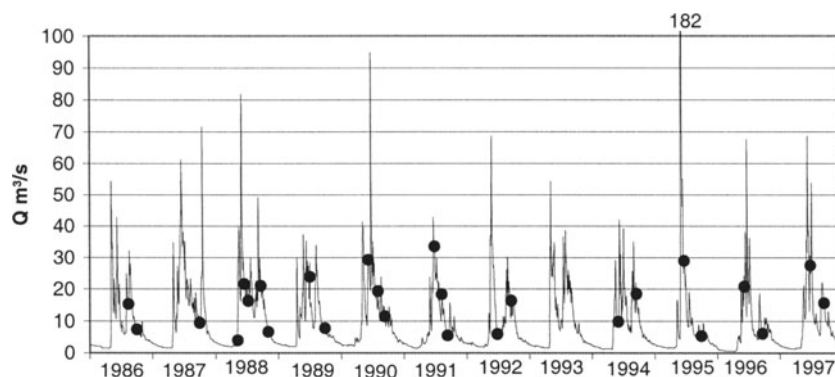


Figure 2. Average daily discharge 1986–97 at the outlet of Lake Atnsjøen (NVE discharge station 2.32.0.1001.0). Periphyton sampling dates are indicated.

tary Setninga, where the calcium content is around 3 mg l^{-1} . Alkalinity and pH more or less follow the same pattern.

Methods

Sampling of periphyton for qualitative observations followed the method described in Jarlman et al. (1996). This includes surveying with aqua-scope a defined area/river stretch (10 m along the river and as far from shore as possible), abundance estimates of all macroscopically visible elements (percent cover of the surveyed area), and sampling of the elements in separate vials (Table 3). Transects for observation of percent cover of macroscopic algae and mosses were established in 1990. All transects were marked by iron rods, landmarks, boulders etc (Lindstrøm & Johansen, 1997). Since 1990, abundance estimates have been based on visual assessment of percent cover within a frame ($50 \times 50 \text{ cm}$) placed at the bottom and moved along the transects.

Microscopic organisms were collected according to a standard method (Kelly et al., 1998). Ten stones with median diameter 10–20 cm were collected randomly in the sampling area. From each stone an area of 8 by 8 cm on the upper side was brushed off with a toothbrush, mixed in a jar with 1 litre water, and a subsample taken. All samples were preserved in the field with formaldehyde (2–4%) and stored at the Norwegian Institute for Water Research.

The samples were examined in a stereoscopic microscope for screening and sorting and in a research microscope for species identification. Abundance estimates of microscopic species were done by estimation of frequency in at least two parallel microscope

slides and presented as frequent (xxx), common (xx) or rare (x). Abundance of macroscopic elements was estimated in the field.

The species were identified according to identification keys listed in Lindstrøm (1989) and Lindstrøm & Johansen (1997) (Tables 4 and 5). Nomenclature for macroscopic species followed Tolstoy & Willén (1997). Revisions in the order Croococcales (Cyanobacteria) were according to Komárek & Anagnostidis (1999). Species in the order Desmidiaceae (Charophyceae) were only identified to genus. Many filamentous green algae can only be identified to species in the fertile stage. As they are usually only found sterile, they have been named by their generic name and a number and/or letter (Table 5). This refers to a description based on vegetative characteristics (unpublished data). Samples of these algae are kept in a collection at the Norwegian Institute for Water Research. A similar approach was taken by Israelson (1949) in his naming of some zygnetacean algae. He stated that these species rarely are fertile in Scandinavian watercourses. All algae collected in our survey that correspond to his descriptions are named according to his terms (generic name and a letter, Table 5).

We addressed epilithic cyanobacteria and algae (except diatoms) and species living epiphytic on epilithic algae and submerged bryophytes. The most common groups, cyanobacteria and green algae, were used to illustrate variations and trends in species composition and diversity. Species diversity is in this context expressed as number of taxonomic units, as presented in Tables 4 and 5. The term ‘character species’ is used for organisms that are present regularly, often in large numbers, and obviously possess a natural propensity to thrive in the particular watercourse/river stretch.

Table 2. Chemical characteristics of River Atna, based on 12 measurements yearly 1986–96 (mean, max-min; Blakar & Digernes, 1989; 1993; 1999; Blakar, 1994; Blakar et al., 1997). All data marked with * were collected outside the regular observation program and are based on 2–3 measurements in September 1992 and 1994 (unpubl. data) (St.1 Vidjedalsbekken and st.7 River Setninga, and all TOC (total organic carbon) and tot-P data).

Station	Ca (mg l ⁻¹)	Alkalinity (μekv l ⁻¹)	pH	Cond (μS cm ⁻¹)	TOC (mg l ⁻¹)	totP-P (μg l ⁻¹)	NO3-N (μg l ⁻¹)
st.1* Vidjedalsbekken	0.6* (0.5–0.75)	23* (0–20)	6.2* (6.0–6.4)	8* (5–17)	0.5*	2*	94*
st.2 Dørålen	0.5 (0.4–1.3)	10 (0–20)	5.6 (5.0–6.3)	8 (5–15)	0.5*	2*	120 (5–210)
st.3 Elgvassli	0.7 (0.5–1.5)	20 (0–40)	5.8 (5.0–6.4)	9 (6–25)	1.0*	3*	100 (0–190)
st.5 Outlet Lake Atnsjøen	0.9 (0.8–1.3)	26 (10–50)	6.1 (5.7–6.6)	11 (6–18)	1.2*	4*	95 (0–160)
st.7* River Setninga	3.2* (1.5–2.7)	180* (40–120)	7.0* (6.8–7.2)	23* (18–30)	1.2*	5*	50*
st.8 Solbakken	1.7 (1.5–2.7)	80 (40–120)	6.7 (6.4–7.0)	15 (12–25)	1.35*	4*	80 (0–180)

Current velocity was measured with a Schiltknecht Micro-Mini propeller; type 642 w-m/l, 2–5 cm above the riverbed along the periphyton transects.

The data matrix (species on rows, samples on columns), in which only species identified to species or generic level were included, was analysed with correspondence analysis method (Hill, 1973; Palmer, 1993). This method, also called reciprocal averaging, is an ordination technique with which sites (i.e. samples, localities) and/or species can be arranged along environmental gradients (Palmer, 1993). The method is based on the assumption that the data have a unimodal response to a gradient. In its basic form correspondence analysis produces two sets of so-called scores, one for sites and one for species. These scores can directly be used in ordination. For example, the site scores (one value per site) characterise the species composition of a particular site with a single number, and the differences in the site scores indicate differences in species composition between the sites. In other words, site scores serve as an ordination index based on the species composition of the sites. For more detailed description of the correspondence analysis method and its calculation algorithm, see e.g. Palmer (1993).

As the results from correspondence analysis may be sensitive to inclusion/exclusion of rarely observed species, two different versions of the original data mat-

rix were analysed: V1) a data matrix in which all rows and columns of the original matrix (with non-zero row/column sum) were taken into the analysis, and V2) a data matrix in which all species observed in less than 4 samples (20% of the species) and all samples counting less than 4 species (5% of the samples) were removed from the original matrix before correspondence analysis. The distribution of scores as well as the results shown in Fig. 6 and Table 6 remained qualitatively similar between the two approaches.

The site scores obtained from correspondence analysis (original matrix, V1) were then plotted versus the time of sampling, and versus environmental factors measured at each station (Fig. 6). Due to missing chemical data in st.6 Sollia, data from the upstream st.5 Outlet Lake Atnsjøen were used. A linear regression line was fitted to the plots of time or environmental factor versus the site scores from the correspondence analysis.

A similarity index (S) based on qualitative data was calculated to validate inter-annual variation in species composition within a given station (Sørensen, 1948):

$$S = \frac{C}{A + B},$$

where A is number of species at st. A; B is number of species at st. B, and C is number of species found at both st. A and st. B. The index varies between 1

Table 3. Periphyton sampling programme in River Atna 1986–1997. S: Qualitative samples, M: Manual transect analyses, P: Underwater photography.

Date	st.1 Vidjedals-bekken	st.2 Dørålen	st.3 Elgvassli	st.5 Outlet Lake Atnsjøen	st.6 Sollia	st.7 River Setninga	st.8 Solbakken
860813	S	S	S	S			S
861001	S	S	S	S			S
870930		S	S		S	S	S
880615		S	S			S	S
880919		S	S		S	S	S
890701	S	S	S	S	S	S	S
890927	S	S	S		S	S	S
900606	S	S	S M		S	S	S
900802	S M	S M	S M		S M		S M
900911	S	S M	S M		S M	S M	S M
910626	S	S M	S M		S M	S M	
910808			M		M	M	M
910910		S M	S M		S M	S M	S M
920626	S M	S M	S M		S M	S M	S M
920915	S	S	S M		S M	S M	S M
940531	S M	S M P	S M P	S P	S M P	S M P	S M P
940913	S M	S M P	S M P	S P	S P	S P	S M P
950619		P	P	P	P	P	P
950927	S	S M P	S M P	S P	S M P	S M P	S M P
960605	S M	S M P	S M P	S M P	S M P	S M P	S M P
960919	S M	S M P	S M P	S M P	S M P	S M P	S M P
970627	S M	S M P	S M P	S M P	S M P	S M P	S M P
970916	S M	S M P	S M P	S M P	S M P	S M P	S M P

(perfect similarity in species composition) and 0 (no similarity).

Correlation between species diversity and environmental variables was analysed in a scatter by linear regression.

Material

Table 3 shows the sampling program from 1986 to 1997. Periphyton was sampled twice a year to intercept seasonal variations, in spring (mainly June) and early autumn (mainly mid September).

Initially the observations focused on qualitative aspects. Quantitative aspects were studied briefly, by estimates of percent cover of macroscopic species at the sampling sites. Due to extremely variable es-

timates of percent cover during the years 1986–89 (Lindstrøm & Johansen, unpubl. data), a more precise quantitative observation programme was initiated. Transect analyses were started in 1990, and underwater photography in 1994. The locality at the outlet of Lake Atnsjøen (st.5) that had been surveyed in 1986 and 1989, was included in the sampling programme from 1994 to provide information about periphyton abundance and seasonal variation in a physically more stable site than the six other sampling sites.

Station 7 in River Setninga was moved 1km upstream in 1994, to allow for underwater photography. The initial site had some large boulders in the riverbed that made it unsuitable for underwater photography. There is no reason to believe that climate, hydrology or water chemistry are different at the two stations.

Table 4. Attached cyanobacteria identified in samples from River Atna 1986–97.

Organisms	Comments on appearance, habitat, and frequency. Character species marked with – C
Cyanophyta:	
<i>Aphanocapsae</i> sp.	among other algae, not common
<i>Calothrix fusca</i> Bornet et Flahault	among other algae, not common
<i>Calothrix gypsophila</i> (Kützing) Thuret	C – dark tufts on rocks (includes <i>C. orsiniana</i> Thuret nova comb. Bourelly)
<i>Calothrix ramenskii</i> Elenkin	C – dark tufts or feltlike cover
<i>Calothrix braunii</i> Bornet et Flahault	among other algae, not common
<i>Calothrix</i> spp.	occasional, probably more species
<i>Clastidium cylindricum</i> Whelden	occasional, epiphytic on other algae
<i>Clastidium rivulare</i> (Hansgrig) Hansgrig	thin cover on stones
<i>Clastidium setigerum</i> Kirchner	C – epiphytic, on other algae
<i>Chamaesiphon confervicolus</i> A. Braun	epiphytic on algae and mosses
<i>Chamaesiphon rostafinskii</i> Hansgrig	C – epiphytic, on algae and mosses
<i>Chamaesiphon fuscus</i> (Rostafinski) Hansgrig	C – dark brown ‘paint’ spots on big rocks
<i>Chamaesiphon minutus</i> (Rostafinski) Lemmermann	C – epiphytic, on other algae
<i>Chamaesiphon subglobosus</i> (Rostafinski) Lemmermann	epiphytic, on mosses and algae
<i>Chamaesiphon</i> sp. (colonny)	epilitic on rocks
<i>Choococcus</i> sp.	occasional, among other algae
<i>Cyanophanon mirabile</i> Geitler	C – epiphytic, on other algae
<i>Gloeocapsopsis magma</i> (Breb.) Komarek et Anagnostidis	epilitic among other cyanobacteria
<i>Homoeothrix varians</i> Geitler	among other algae
cf. <i>Leptolyngbya perelegans</i> (Lemmermann) Anagnostides et Komàrek	among other algae
<i>Lyngbya kützingii</i> Schmidle	among other algae
<i>Merismopedia punctata</i> Meyen	among other algae
<i>Nostoc verrucosum</i> Vaucher ex Bornet et Flahault	small warty balls, epilitic, close to the river bank
<i>Oscillatoria</i> sp1 (NIVA-col.)	(diam. 7–9µ, granulated cross walls) - single trichomes among other algae
<i>Phormidium autumnale</i> (Agardh) Gomont	C – dark, olive green, shiny cover with ‘nerves’, on stones,
<i>Phormidium hetropolare</i> Skuja	C – between other algae
<i>Phormidium</i> sp1 (NIVA-col.)	(diam. 2–3µ, bright green) between other algae
<i>Phormidium</i> sp2 (NIVA-col.)	C – (3–4µ, pale green) single short fragments on rocks and among other algae
<i>Phormidium</i> sp3 (NIVA-col.)	(diam. 2–4µ, bright blue green) differs from sp2 by collar
<i>Pleurocapsae</i> sp.	brown to yellowish, among other algae
<i>Rivularia biasolettiana</i> (Meneghin) Bornet et Flahault	C – small dark blue green balls, close to the river bank
<i>Schizothrix</i> cf. <i>latierita</i> (Kützing) Gomont	C – tufts, reddish to grayish tufts, often among other algae
<i>Schizothrix</i> sp. (diam. 2µ, yellow sheats)	occasional
<i>Scytonematopsis starmachii</i> Kovàcik et Komàrek	C – dark brown, ‘dry’ spots/cover on bedrock/big stones, periodically aerated
<i>Stigonema mamillosum</i> (Lyngbye) Agardh	C – tufts/felt on bedrock/big stones, periodically aerated
<i>Stigonema hormoides</i> (Kützing) Bornet et Flahault	brownish to yellowish, among other algae
<i>Stigonema</i> sp.	occasional
<i>Toylypotrix distorta</i> Kützing	C – dark blue green small tufts on big rocks
<i>Tolypothrix penicillata</i> Thurnet	C – olive green small tufts on big rocks
Unidentified coccoid cyanobacteria	occasional
40 taxa of cyanobacteria	

Table 5. Attached algae, except cyanobacteria (Table 4) and diatoms, identified in samples from River Atna 1986–97. diam. = filament diameter, K = number of chloroplasts, L = lens shaped cross walls, R = reticulate cross walls.

Organisms	Comments on appearance, habitat and frequency. Character species marked with – C
Chlorophyta:	
<i>Binuclearia tectorum</i> (Kützing.)Berger	among other filamentous algae
<i>Bulbochaete</i> spp.	C – bright green tufts, mostly on rocks close to river bank, 1 species identified: <i>B. intermedia</i> var. <i>depressa</i> Witrock
<i>Closterium</i> spp.	only few species identified, not very common
<i>Cosmarium</i> spp.	only few species identified, quite common
<i>Drapharnaldia glomerata</i> (Vaucher) C.Agardh	seldom, common on st. 6 Sollia in 1996
<i>Euastrum</i> spp.	only few species identified, not common
<i>Geminella</i> sp.	seldom
<i>Gongrosira</i> cf <i>lacustris</i> Brand	C – blackish spots on big rocks
<i>Gymnozyga</i> sp.	occasional
<i>Hyalotheca dissiliens</i> (Smith) Brebisson	seldom, among other filamentous algae
<i>Klebsormidium flaccidum</i> (Kützing) Silva, Mattox et Blackwell	intensely green filaments, on rocks
<i>Klebsormidium rivulare</i> Morison et Sheat	C – intensely green filaments, on rocks, in swift current
<i>Klebsormidium montanum</i> (Skuja) S.Watanabe	rare, found together with <i>K. rivulare</i> (separation of the 2 species difficult)
<i>Microspora amoena</i> (Kützing) Rabenhorst	(C) – cell diameter 22–26µ, laminated walls, visible H-shaped cross walls, chloroplast cover cellwall, on rocks and mosses
<i>Microspora</i> cf. <i>lauterborni</i> Schmidle	occasional
<i>Microspora palustris</i> var <i>minor</i> Wichman	C – intensely green filaments, on rocks, seldom on mosses, mostly close to the river bank
<i>Mougeotia</i> a (according to Israelson 1949)	C – green filaments, among other algae on mosses/rocks (diam. 3–6µ, L/B<10)
<i>Mougeotia</i> a1 (according to Israelson 1949)	broad than the above given species (diam. 10–12µ, long cells)
<i>Mougeotia</i> a/b (according to Israelson 1949)	C – green filaments, among other algae (diam. 12–14µ, short cells)
<i>Mougeotia</i> sp.	(diam 17–20µ)
<i>Mougeotia</i> d (according to Israelson 1949)	(diam. 25–30µ) – see next, broad forms can be difficult to separate
<i>Mougeotia</i> e (according to Israelson 1949)	C – bright green filaments, on mosses and rocks (diam. 30–37µ)
<i>Mougeotiopsis calospora</i> Palla	filaments among other algae
<i>Oedogonium</i> a (NIVA-col.)	C – green filaments, among other algae (diam. 3–10µ)
<i>Oedogonium</i> b (NIVA-col.)	green filaments, among other algae (diam. 14–18µ)
<i>Oedogonium</i> c (NIVA-col.)	C – green filaments, on mosses and rocks (diam. 24–29µ)
<i>Oedogonium</i> d (NIVA-col.)	C – green filaments, on mosses and rocks (diam. 28–35µ)
<i>Penium</i> spp.	only few attempts to identify, not very common
<i>Protoderma viride</i> Kützing.	epiphytic on other algae and mosses
<i>Schizochlamys gelatinosa</i> A.Braun	gelatinous layers on rocks and among other algae
<i>Spirogyra</i> sp1 (NIVA-col.)	(15–18µ, 1K,R.) among other algae
<i>Spirogyra lapponica</i> (Lemmermann) Lemmermann	C – green filaments, on rocks and lying loose in eddies (diam. 24–29µ, 1K,L), called <i>S. lapponica</i> according to Israelson (1949)
<i>Spirogyra</i> a (according to Israelson 1949)	(diam. 30–37µ, 1K,L) – green filaments, mostly on mosses
<i>Spirogyra</i> d (according to Israelson 1949)	(diam. 60–70µ, ?K,L) – many chloroplasts – may be <i>S. majuscula</i> Kützing
<i>Staurodesmus</i> sp.	only few species, not common
<i>Teilingia granulatum</i> (Roy et Biss.) Bourrelly	filaments, among other algae
<i>Ulothrix zonata</i> (Kützing) Weber	C – dark green horizontal bands on big rocks, in the upper littoral zone
cf. <i>Zygnema</i> a (according to Israelson 1949)	(diam. 17–22µ) bright green filaments, mostly on mosses
<i>Zygnema melanosporum</i> Lagerheim	C – bright green filaments, mostly on mosses in the current, (diam. 22–26µ), called <i>Z. melanosporum</i> according to Israelson (1949)
Unident. <i>Chaetophorales</i> , developmental stage	occasional
Unident. coccoid green algae	occasional
42 taxa of green algae	

Continued on p. 71

Table 5. Continued.

Organisms	Comments on appearance, habitat and frequency. Character species marked with – C
Chrysophyta	
<i>Hydrurus foetidus</i> (Villars) Trevisan	C – yellowish to brown gelatinous tufts on rocks, mainly in swift current
<i>Hydrurus foetidus</i> – not fully developed, only cell aggregates and cysts	C – yellowish to brownish thin cover on rocks
1 chrysophyte taxon	
Rhodophyta	
<i>Batrachospermum gelatinosum</i> (L.) De Candolle	blue green to gray green gelatinous tufts, on rocks
<i>Lemanea condensata</i> Israelson	C – green to yellowish 1-3 cm long hairs in tufts on big rocks, in strong current
<i>Lemanea fucina</i> Bory	C – brown to greenish hairs on big rocks, in strong to median current
<i>Lemanea</i> sp. (Chantransia stages)	occasional on rocks, often together with other algae
<i>Audouinella pygmaea</i> (Kützinger) Weber-Van Bosse	brownish tufts, mostly on mosses
5 taxa of red algae	

Results

The algal flora

All taxa of cyanobacteria and algae (except diatoms) observed 1986-97 are listed in Tables 4 and 5. A total of 40 taxa of cyanobacteria were recorded, 16 were found regularly in significant quantities in one or more sampling stations and were termed 'character species' (Table 4). The green algae (Chlorophyceae) were represented by 42 taxa, of which 13 were termed 'character species' (Table 5). Only one taxon of Chrysophyceae was recorded. Among the five taxa of Rhodophyceae, two were termed 'character species' (Table 5). Only minor changes in species composition have been observed since the first comprehensive analysis of data in 1989 (Lindstrøm 1989). The algal flora is characterised by species that grow well in clear unpolluted water with low conductivity and low nutrient content (Israelson, 1949; Backhaus, 1968; Kann, 1978; Wehr, 1979; Johansson, 1982; Lindstrøm, 1992; Rai & Gaur, 1994; Rott et al., 1997; Schmedtje & Bauer, 1998; Lindstrøm, 2000).

Most of the algal flora exhibited substantial differences in occurrence and abundance along the river. The following sections describe some 'character species' in terms of morphology, taxonomy and occurrence (Figs 3 and 4).

Longitudinal distribution - cyanobacteria

Phormidium sp2 (NIVA-col.)

An unidentified *Phormidium* occurred regularly in small numbers at the upper station, st.1 Vidjedalsbekken, and occasionally along the main river. The filament (diam. 3–4 µm) is short (25–200 µm), has pale blue-green colour and cell length is shorter than cell diameter. It has few diagnostic characteristics. It occurs as a thin cover on stones together with diatoms, mainly *Diatoma mesodon* (Ehrenberg) Kützinger, *Achnanthes marginulata* Grunov and some species of *Eunotia*.

Phormidium autumnale (Agardh) Gomont

P. autumnale was found regularly as a shiny dark blue-green cover on stones in the current from st.1 Vidjedalsbekken and downward (not shown in Fig. 3). It was the only cyanobacteria forming macroscopically visible growth at st.1. It was seldom found in the upper river in spring, further down it occurred in both spring and autumn. The abundance varied substantially between years.

Chamaesiphon subglobosus (Rostafinski) Lemmermann

The only other cyanobacteria observed regularly at st.1 Vidjedalsbekken, was *C. subglobosus*. The description given in Komárek & Anagnostidis (1999) fits well to the species found in Vidjedalsbekken. It grew on

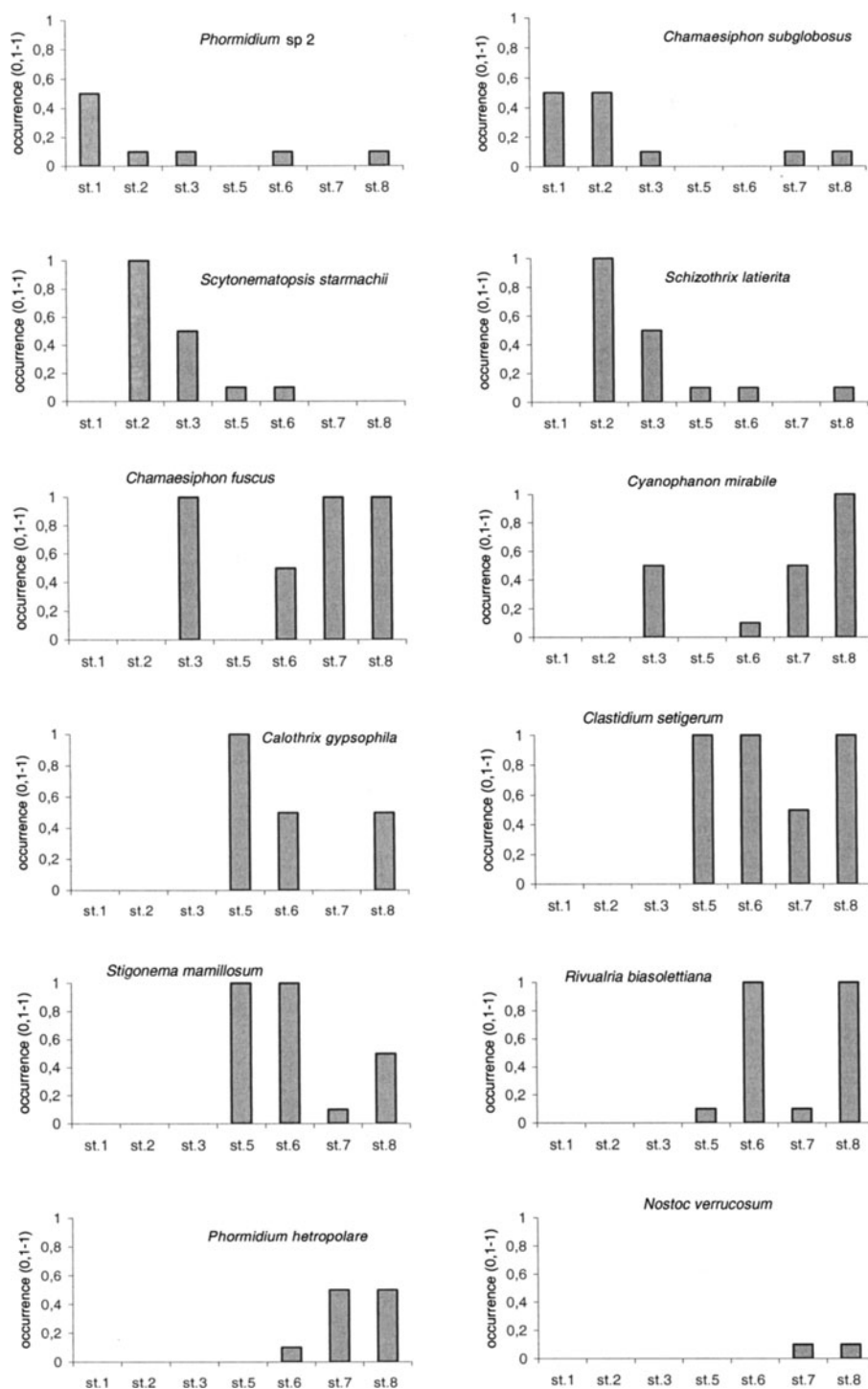


Figure 3. Distribution and occurrence of selected species of cyanobacteria along River Atna, averaged for the period 1986–97. Occurrence is given as 0.1 = occasional, 0.5 = occurring regularly, 1 = common.

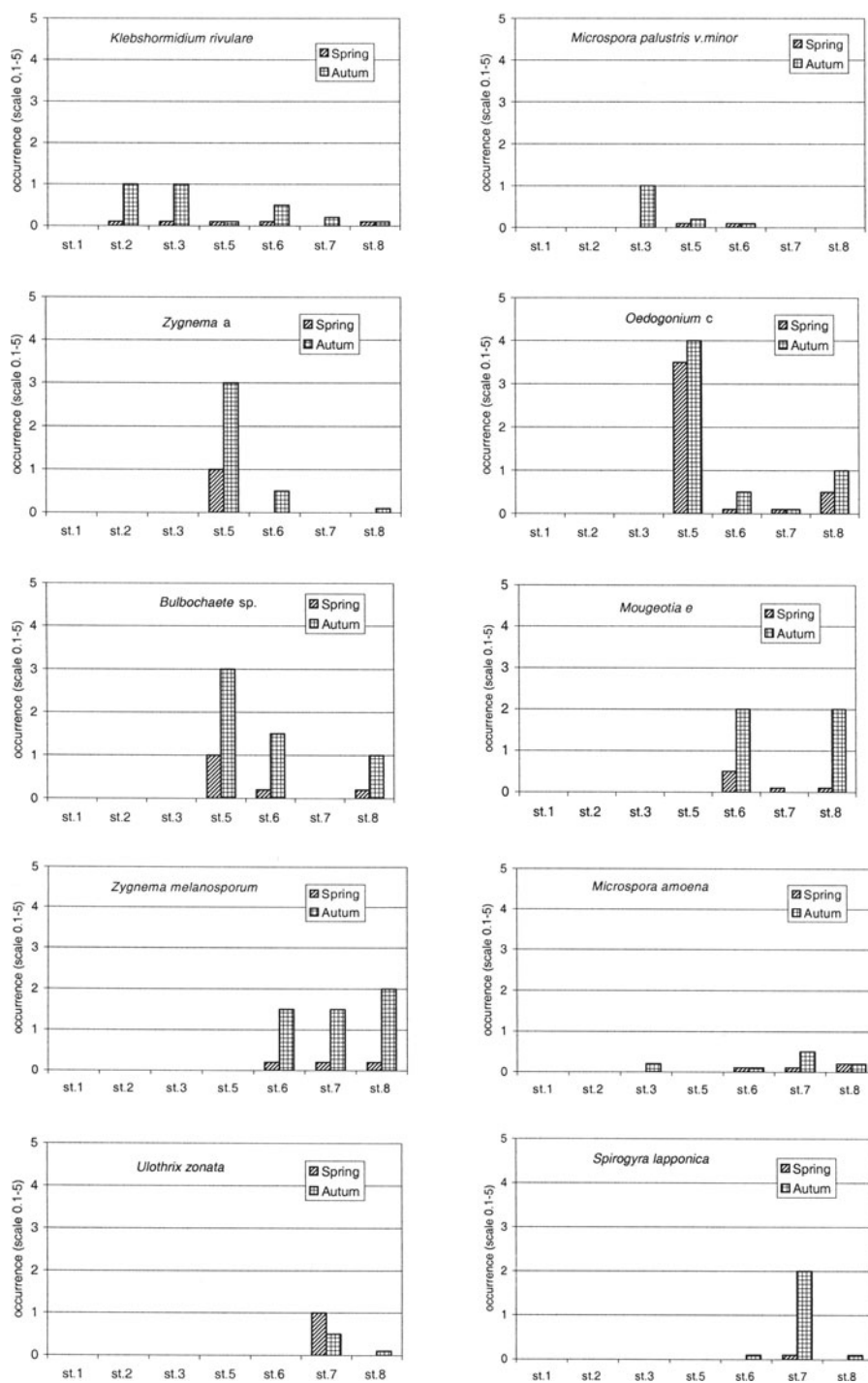


Figure 4. Distribution of selected species of filamentous green algae along River Atna, averaged for the period 1986-97. Occurrence (percent cover of the riverbed/transect) is given as: 0.1 = occasional, 0.5 = $\leq 1\%$, 1 = 1–5%, 2 = 5–12%, 3 = 12–25%, 4 = 25–50%, 5 = $\geq 50\%$.

Table 6. R^2 and p -values of the regression lines for the site score versus temporal and environmental factors (see Fig. 6). Note that with the three first factors marked with asterisk superscript (*) normalized site scores are used (site score normalised by subtracting the mean value from the stations' site scores). The values correspond to analysis with original data matrix (version V1), while values in parentheses correspond to the results from the alternative analysis in which species observed in less than 4 samples and samples including less than 4 species were omitted in correspondence analysis (matrix version V2).

Factor	R^2 of the regression line	p value of the regression line
Season (day of the year)*	0.150 (0.119)	<0.001 (<0.001)
Day number in 1986–1997 (all seasons)*	0.033 (0.026)	0.043 (0.082)
Day number in 1986–1997 (autumn only)*	0.122 (0.086)	0.003 (0.014)
Altitude	0.736 (0.704)	<0.001 (<0.001)
Growth period length	0.677 (0.616)	<0.001 (<0.001)
Calcium	0.222 (0.184)	<0.001 (<0.001)
Alkalinity	0.157 (0.130)	<0.001 (<0.001)
pH	0.356 (0.382)	<0.001 (<0.001)
Conductivity	0.272 (0.235)	<0.001 (<0.001)
TOC	0.636 (0.621)	<0.001 (<0.001)
Tot-P	0.653 (0.632)	<0.001 (<0.001)

stones and on the only common bryophyte in Vidjedalsbekken, *Hygrohypnum alpestre* (Hedw.) Loeske. It occurred regularly in the main river at st.2 Dørålen, but was otherwise rare.

Scytonematopsis starmachii Kovàcik et Komàrek

This cyanobacteria formed distinctive dark brown spots or continuous cover on large stones and boulders along the riverbank, in the periodically aerated zone at st.2 Dørålen. The coverage was reduced after large floods, but was otherwise relatively stable. It occurred regularly, but only in small numbers, at the downstream st.3 Elgvassli (mostly together with other algae) and at the outlet of Lake Atnsjøen (st.5), but was otherwise rare. *S. starmachii* was first described from the Tatra mountains by Kovàcik & Komàrek (1988). They suggested that this highly characteristic, but variable algae had previously been overlooked. They assumed that it would occur in oligotrophic, clear and somewhat acidic waters in mountain areas. The distribution of *S. starmachii* in Norway confirms this. The species is characteristic of the upper pristine part of the watercourses, it prefers running water (although it may be found in lakes), and seems to be restricted to clear, nutrient poor, weakly acidic water (Lindstrøm, 1992; 2000; unpubl. data).

Schizothrix cf. latierita (Kützinger) Gomont

S. latierita was the other cyanobacteria that characterised st.2 Dørålen. When fully developed it was recognised as a brownish felt on rocks. It could also be seen as reddish to greyish small tufts among other algae. It was found regularly, but in smaller quantities downstream in the main river. The species identity is somewhat uncertain, it is similar to other species of *Schizothrix*.

Chamaesiphon fuscus (Rostafinski) Hansgrig

C. fuscus was found from st.3 Elgvassli and downstream in the river, as characteristic dark brown 'paint spots' or crusts on large rocks, preferably on the downstream side, sheltered from sediment erosion. The cover of the substratum surface seldom exceeded a few percent. It was mostly submerged, but may be exposed at low discharge.

Cyanophanon mirabile Geitler

This characteristic small epiphyte grew on a number of other algae. It occurred regularly from st.3 Elgvassli and downwards and could be quite common at st.8 Solbakken, particularly in the autumn. It was never found at the upper stations Vidjedalsbekken (st.1) and Dørålen (st.2).

Calothrix gypsophila (Kützinger) Thuret

This alga, a character species in the outlet of Lake Atnsjøen (st.5), formed a dark felt on stones together with other oligotrophic, slow growing cyanobacteria. It occurred regularly in the lower part of the main river, but was never found upstream of the lake. It lived close to the riverbank or in other sheltered areas such as the downstream side of large rocks. It was most common in the autumn. *C. gypsophila* varies in its visual characteristics and may sometimes be quite similar to *Dichothrix orsiniana* Born. et Flah., described in detail by Skuja (1964). In this condition it has long richly branched filaments and the sheets are longer and more distinctly layered than the typical *C. gypsophila*. The observations support the hypothesis discussed by Golubic (1967), Kann (1978) and others, that *C. gypsophila* and *D. orsiniana* (syn. *Calothrix orsiniana* Thuret) are growth forms of the same species.

Clastidium setigerum Kirchner

This typical small epiphyte was common from the outlet of Lake Atnsjøen (st. 5) and downstream. It may occur on various algae, but seemed to prefer filamentous green algae. Two other *Clastidium*-species were found occasionally, *C. cylindricum* and *C. rivulare*.

Stigomena mammosum (Lyngbye) Agardh

The distribution of this characteristic alga was similar to *C. setigerum*, i.e. in the lower part of the main river and occasionally in the tributary Setninga (st. 7). Like other slow growing cyanobacteria in River Atna, it occupied physically sheltered places where it formed a dark brown felt. The felt appeared shorter in River Atna than in more stable physical environments. It may be exposed during periods of low flow.

Rivularia biasolettiana (Meneghin) Bornet et Flahault

R. biasolettiana was found in small numbers on physically sheltered places from Lake Atnsjøen (st. 5) and downstream. It formed typical soft round balls (diameter max 0.5 cm) without recognisable calcium incrustations, as found in the similar *R. haematites* (D.C.) C.A. Agardh.

Phormidium hetropolare Skuja

P. hetropolare appeared in autumn samples as single filaments among other algae. The description given by Skuja (1964) fits well with the species found in River Atna. It was recorded from st.6 Sollia and downstream.

Nostoc verrucosum Vaucher ex Bornet et Flahault

N. verrucosum was found in small numbers in the tributary Setninga (st.7) and occasionally downstream in the main river. Typical, fully developed specimens formed small warty balls or lumps as described for *N. verrucosum* (Mollenhauer et al., 1999). Species with a smooth outer appearance, like *N. sphaericum* Vaucher, may also be found.

Most of the other cyanobacteria occurring regularly (e.g. *Chamaesiphon rostaefinskii* Hansgrig, *Calothrix ramenskii* Elenkin, *Tolypothrix penicillata* Thuret) had a similar limited distribution along the watercourse and add to the impression of zonation along the river.

*Longitudinal distribution – filamentous green algae**Kelbshormidium rivulare* Sheat et Morison

No filamentous green algae occurred regularly in the upper tributary st.1 Vidjedalsbekken, and only one species, *K. rivulare*, occurred regularly at the uppermost station in the main river st.2 Dørålen. It could be seen in September as small, bright green tufts, apparently growing directly on stones in the current. It was hardly observed in June and its abundance in terms of substratum cover in September rarely exceeded 1%. A similar occurrence was recorded at the downstream station, st.3 Elgvassli. The species may be found further downstream in the river, in small quantities among other algae.

Microspora palustris var *minor* Wickman

This thin (diam. 8–10 µm) green alga fits well with Wickman's (1937) description. It appeared in the autumn at st.3 Elgvassli, on places exposed to the sun and close to the riverbank, where the water is warmed up periodically. It was never found during spring at Elgvassli, but may be found in small quantities among other algae at downstream sites, in both spring and autumn. It is commonly found in early summer in lowland rivers in Southern Norway (Lindstrøm & Johansen, 2001).

Zygnema a (Israelson 1949)

This belongs to the filamentous green algae that Israelson described by vegetative characters (mainly general appearance and cell width) because they rarely occur in a fertile stage. The present *Zygnema* (diam. 17–22 µm) is similar to Israelson's *Zygnema* a. Confusion with other similar zygnematacean algae is however

possible. It appeared as bright green tufts in the current, in permanently submerged areas, mainly attached to mosses growing on the stones. It was common in the outlet of Lake Atnsjøen (st.5), but was otherwise occasional. Like most of the filamentous green algae, the coverage of the riverbed was distinctly higher in autumn than early summer.

Oedogonium c (NIVA-col)

Like the zygnematacean algae, most members of the genus *Oedogonium* must be fertile to be identified. A separation of the species into different categories is based on general appearance and cell width (unpublished data). *Oedogonium* c (cell with 24–29 μm) covered almost the entire riverbed in the deep middle zone in the outlet of Lake Atnsjøen (st.5), reaching up to 80% in the autumn. It was also present regularly in spring in this permanently submerged zone, which is seldom disturbed physically by floods or ice scouring. *Oedogonium* c was found regularly downstream in the main river.

Bulbochaete spp.

A third species of filamentous green algae, *Bulbochaete*, may cover large areas at the outlet of Lake Atnsjøen (st. 5). It grew close to the riverbank in areas temporarily exposed to open air. Abundance in the autumn was much higher than in early summer. It occupied similar habitats downstream in the main river. At least one species of *Bulbochaete*, *B. intermedia* var. *depressa* Wittr., has been identified from River Atna. Like most filamentous green algae in Norwegian watercourses, *Bulbochaete* is seldom found in a fertile stage.

Mougeotia e (Israelson, 1949)

Mougeotia e has broader filaments (diam. 30–37 μm) than other *Mougeotia* species found in Norwegian waters and is therefore easily recognised. It grew attached to mosses, as bright green tufts in the current, from st.6 Sollia and downstream. It could be found in early summer, but was always more common in the autumn.

Zygnema melanosporum Lagerheim

This *Zygnema* was found fertile a few times and identified as *Z. melanosporum*. All findings of similar, but sterile, *Zygnema* (diam. 22–26 μm) are supposedly the same species. Similar to *Mougeotia* e, it grew attached to mosses, as bright green tufts in the current, from st.6 Sollia and downstream. *Oedogonium* c, *Mougeotia* e, and *Zygnema melanosporum* were often found together.

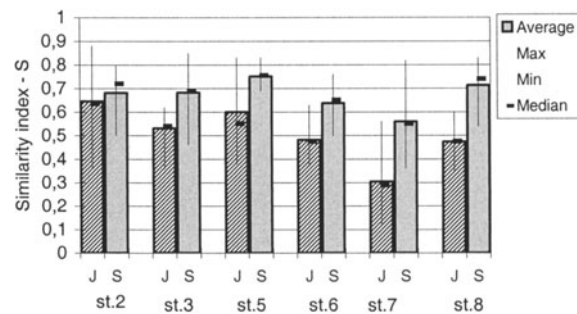


Figure 5. Similarity-index (Sørensen, 1948) based on species composition of cyanobacteria and green algae, calculated for samples collected at the same station in June (J) and September (S), River Atna 1986–97.

tia e, and *Zygnema melanosporum* were often found together.

Microspora amoena (Kütz.) Rabenh.

M. amoena was found regularly in the autumn in the tributary Setninga (st.7). The occurrence was otherwise irregular, and mostly among other algae.

Ulothrix zonata (Kütz.) Weber

U. zonata was found regularly in the tributary Setninga (st.7) and occasionally in the main river downstream the confluence of River Setninga and River Atna. It formed narrow bands on large rocks in the splash zone, in spring and early summer. It may also be found in late September and October.

Spirogyra lapponica (Lemmermann) Lemmermann

This *Spirogyra* (diam. 24–29 μm) was found fertile, and findings of similar sterile specimens were assumed to be *S. lapponica*. It was found regularly in River Setninga (st.7), and occasionally in the lower parts of the main river. It was often growing directly on stones and may occasionally be found floating in eddies and backwaters in late autumn.

Longitudinal distribution – other algae

Hydrurus foetidus Trevisan

This cold stenotherm chrysophyte was the only macroscopic alga that occurred regularly at the upper st.1 Vidjedalsbekken, where it may grow to a thick brown gelatinous cover on stones in spring/early summer. Sometimes it was found in small quantities close to the riverbank in late autumn. The occurrence in the downstream river was highly variable and unpredictable. It was often found as a thin yellow cover on stones that had been submerged for some time.

Lemanea condensata Israelson

This small *Lemanea* (1–3 cm long threads) grew on blocks in the torrents from st.3 Elgvassli and downwards in the main river. The abundance was highly variable and unpredictable. The description of *L. condensata* given by Israelson (1942) fits well with the *Lemanea* found in River Atna. In River Setninga another *Lemanea*, *L. fucina* Bory, occurred regularly, also on large blocks in high current velocity.

Temporal variation – species composition

Inter-annual similarity in species composition within a given station was calculated separately for spring and autumn samples according to the similarity index of Sørensen (1948). St. 1 was omitted due to extremely low species number. Similarity index for spring and autumn samples averaged 0.51 and 0.67 respectively (Fig. 5). According to experience with this approach from a considerable number (<200) of samples collected in Norwegian rivers in late summer/early autumn, two samples should be regarded as similar when the index is 0.6 or higher (unpublished data). Consequently, our data suggest that in autumn there is a high degree of similarity from year to year at any one station, except at st.7 River Setninga. The lower similarity index for spring samples cannot be evaluated in a similar manner, as our experience with spring samples is insufficient.

The similarity index was lower at st.7 River Setninga than at the other stations, particularly in spring (Fig. 5). This station was moved 1 km upstream when underwater photography started in 1994. This might have affected species composition. Spring samples collected before (1986–92) or after (1994–97) the station was moved, were more similar than samples from the whole period; similarity index 0.40 (86–92), 0.50 (94–97) and 0.31 (86–97). This suggests that minor physical differences between sites may affect species composition, even if hydrology, climate and water chemistry appears to be identical.

At all stations, the inter-annual similarity within a given station increased from spring to autumn. The increase in the main river, expressed as index units, was between 0.05 at st.2 Dørålen and 0.22 at st.8 Solbakken (Fig. 5). The data from the tributary Setninga (st.7) indicated even higher increase in similarity, 0.27. This supports the general impression that the environmental conditions were more stable and the algal flora better developed in autumn.

Environmental variables and long term trends – species composition

All examined trends were based on the regression lines fitted to the plots of time or environmental factor versus the site scores from the correspondence analysis. All trends (both matrix versions V1 and V2), were significantly different from zero at 95% level of confidence, except the long-term trend with all season data and matrix version V2 ($p = 0.082$). The best fit was achieved with the factors altitude, theoretical growth period, TOC (total organic carbon) and tot-P (total phosphorus) (Table 6). It is worth noting that these factors, among many others, are highly inter-correlated ($|r| > 0.85$, Table 7).

The correspondence analysis identified at least three different communities, one in the upper part (stations 1, 2 and 3; 1150–740 m a.s.l.), one in the middle/lower part (stations 5 and 6; 701–522 m a.s.l.). The third was identified as st.7 in River Setninga (525 m a.s.l.). A possible fourth category was identified as st.8 Solbakken 380 m a.s.l. As shown in Fig. 6C and 6D, there was a close correlation between altitude and tot-P and the periphyton communities.

A significant, but not strong change in species composition ($R^2 = 0.15$), appeared from spring to autumn (Fig. 6A). A similar trend ($R^2 = 0.122$) was evident for long term development of species composition (Fig. 6B). The direction of the temporal trend was towards negative site score values, which means that it pointed towards autumn samples (Fig. 6A), lowland sites (Fig. 6C) and increased tot-P (Fig. 6D). No environmental gradients were studied in such detail that they could be related to these weak trends.

Longitudinal variation – species diversity

Species diversity (number of taxa of cyanobacteria and green algae) increased considerably from the upper st.1 Vidjedalsbekken, to the lower st.8 Solbakken (Table 8). Average number of taxa of cyanobacteria in spring samples was 1.3 at st.1 and 9.3 at st.8. Similar data for autumn samples averaged 3.7 cyanobacteria at st.1 and 10.5 at st.8. No green algae were observed at st.1 in spring, while st.8 had 7.1 taxa on average. Autumn samples averaged 1.1 taxa of green algae at st.1 and 15.1 taxa at st.8.

The diversity increase along the river was most pronounced in spring and more pronounced for green algae than for cyanobacteria. In spring, the average diversity for green algae increased by 446% from

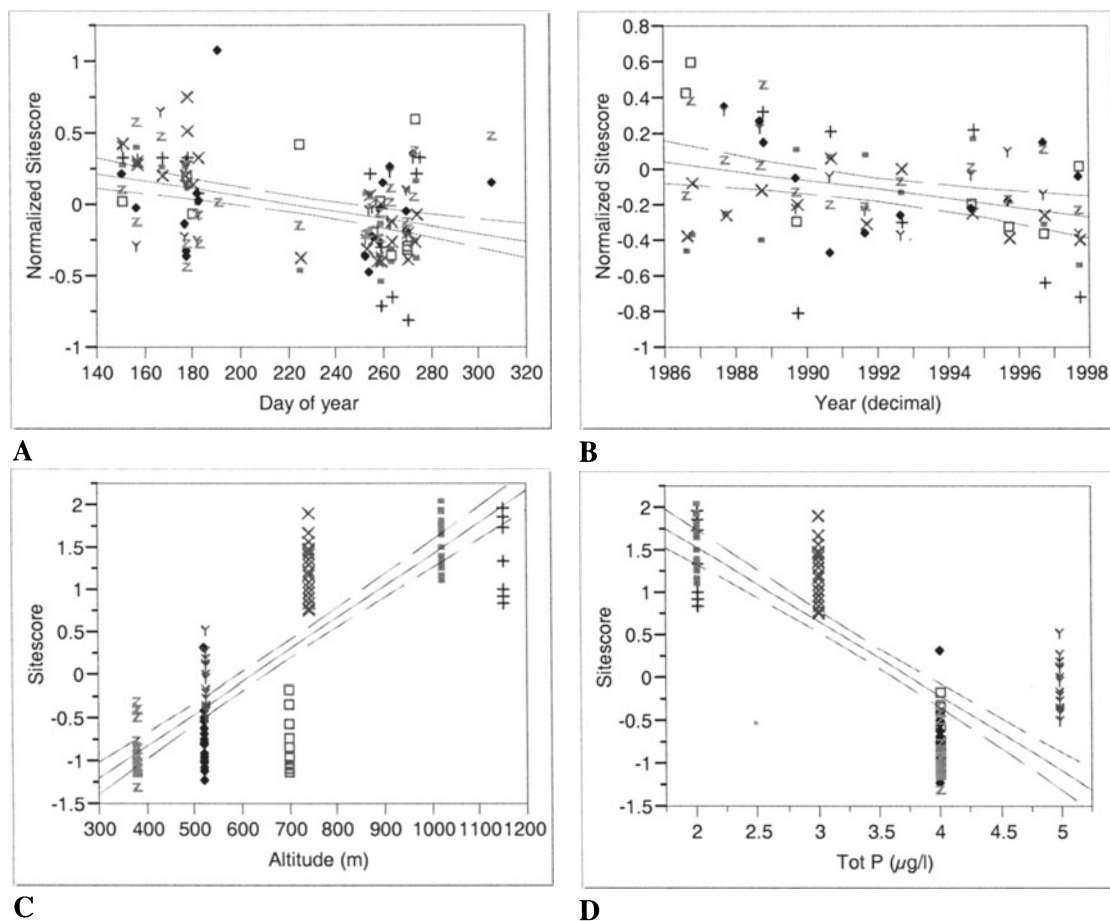


Figure 6. Plots of A) season, B) day number in period 1986-1997 (only autumn samples), C) altitude, and D) total phosphorus concentration versus site scores. In A and B site scores from the correspondence analysis with original matrix (V1) are normalised by subtracting the mean value from the stations' site scores. Stations are denoted as follows: 1(+), 2(■), 3(×), 5(□), 6(◇), 7(Y), 8(Z). The least squares regression line is shown with 95% confidence intervals of the fit.

st.2 Dørålen (no green algae in spring at Vidjedalsbekken) to st.8 Solbakken. The corresponding figure for cyanobacteria (from st.2 to st.8) was 242%. In the autumn, the corresponding increases were 331% for green algae and 169% for cyanobacteria.

Temporal variation – species diversity

Diversity increased from spring to autumn at all stations (Table 8). This was most pronounced for green algae. Average increase in diversity (all sites except st. 1 Vidjedalsbekken) was 145% for green algae and 33% for cyanobacteria. The data may suggest decreasing seasonal variation from the upper to the lower part of the river, but differences between stations were substantial and the data are difficult to evaluate. Seasonal diversity increase of green algae seemed less pronounced at st.5 outlet Lake Atnsjøen (30%), than

at the other stations, (average 169% at stations 2, 3, 6, 7 and 8).

The standard deviation within samples from a given station (Table 8) was higher in spring (average 2, all stations except st.1 Vidjedalsbekken) than in autumn (average 1.45). This suggests that inter annual variability in diversity was more pronounced in spring than in autumn.

Accumulated number of taxa observed in autumn samples remained more or less unaltered after an initial observation period of 3 to 4 years (Fig. 7). Only a very few 'new' taxa were observed in the remaining period. The accumulated number of taxa illustrates the striking differences between sites in species diversity and the increasing significance of green algae downstream. The accumulated taxa of cyanobacteria observed in 1997 were 11 at the upper st.1 Vidjedals-

Table 7. Spearman rank correlation between the different factors. Number of samples $N = 6$ (data from station 6 are omitted). $p < 0.05$ indicates significant correlation at 95% level of confidence.

Variable	by Variable	Spearman rank correlation	p -value
Growth period (days)	Altitude	-0.9856	0.0003
Calsium (mg/l)	Altitude	-0.9276	0.0077
Calsium (mg/l)	Growth period (days)	0.9118	0.0113
Alkalinity (μ -equ/l)	Altitude	-0.7714	0.0724
Alkalinity (μ -equ/l)	Growth period (days)	0.7247	0.1032
Alkalinity (μ -equ/l)	Calsium (mg/l)	0.8986	0.0149
pH	Altitude	-0.6000	0.2080
pH	Growth period (days)	0.5798	0.2278
pH	Calsium (mg/l)	0.7537	0.0835
pH	Alkalinity (μ -equ/l)	0.9429	0.0048
Conductivity (μ S/cm)	Altitude	-0.9276	0.0077
Conductivity (μ S/cm)	Growth period (days)	0.9118	0.0113
Conductivity (μ S/cm)	Calsium (mg/l)	1.0000	0.0000
Conductivity (μ S/cm)	Alkalinity (μ -equ/l)	0.8986	0.0149
Conductivity (μ S/cm)	pH	0.7537	0.0835
TOC (mg/l)	Altitude	-0.9710	0.0012
TOC (mg/l)	Growth period (days)	0.9404	0.0052
TOC (mg/l)	Calsium (mg/l)	0.8956	0.0158
TOC (mg/l)	Alkalinity (μ -equ/l)	0.7945	0.0590
TOC (mg/l)	pH	0.6179	0.1911
TOC (mg/l)	Conductivity (μ S/cm)	0.8956	0.0158
Tot P (μ g/l)	Altitude	-0.8827	0.0198
Tot P (μ g/l)	Growth period (days)	0.8508	0.0317
Tot P (μ g/l)	Calsium (mg/l)	0.9852	0.0003
Tot P (μ g/l)	Alkalinity (μ -equ/l)	0.8827	0.0198
Tot P (μ g/l)	pH	0.7062	0.1168
Tot P (μ g/l)	Conductivity (μ S/cm)	0.9852	0.0003
Tot P (μ g/l)	TOC (mg/l)	0.8636	0.0266

bekken and 24 at st.8 Solbakken. Similar data for green algae were 6 taxa at st.1 and 31 taxa at st.8.

Correlation between diversity and environmental variables

Close covariance between species diversity and duration of the growth period (Fig. 8), altitude, total organic carbon (TOC), and total phosphorous (tot-P) (Table 9) suggests that temperature and nutrients govern species diversity. There was little covariance between pH (and related variables) and species diversity (Table 9).

St.5 outlet Lake Atnsjøen had generally higher diversity than indicated by the regression line in Figure 8. This may be attributed to the more stable

hydrological conditions at the lake outlet than at other sampling sites. Differences in temperature regime between the lake outlet and the river sites may also be important.

At st.7 River Setninga, species diversity was always lower than indicated by the regression lines in Figure 8. The duration of the theoretical growth period was equal at st.7 and the nearby st.6 Sollia (Table 1), but water temperatures were generally 1–2 °C lower in River Setninga (unpublished data). In River Setninga, large deposits of snow in the catchment area may contribute cold water during the whole summer (cf. Tvede, 2004). Moreover, there is no large lake upstream that stabilises the water temperature in this river (Fig. 1).

Table 8. Diversity (cyanobacteria and green algae) in spring (mainly June) and autumn (mid September) at seven sampling stations in River Atna 1986–97.

	Cyanobacteria			Chlorophyceae		
	Average (min–max)	Median	St. dev.	Average (min–max)	Median	St. dev.
St.1 - Vidjedalsbekken						
Spring (<i>n</i> = 8)	1.3 (0–3)	1	0.6	0.0 (0–0)	0	0.0
Autumn (<i>n</i> = 9)	3.7 (1–8)	3	2.4	1.1 (0–6)	0	1.6
Increase spring-autumn (<i>n</i> = 8)	2.4 (0–7)	1	2.5	1.1 (0–6)	0	1.5
%increase	243 %			no green algae in spring		
St. 2 - Dørålen						
Spring (<i>n</i> = 9)	2.8 (1–5)	3	1.3	1.3 (0–3)	1	0.7
Autumn (<i>n</i> = 11)	3.9 (3–9)	3	1.1	3.5 (1–7)	3	1.8
Increase spring-autumn (<i>n</i> = 9)	1.2 (–1–7)	1	2.1	2.2 (–2–6)	2	2.2
% increase	42 %			166%		
St.3 - Elgvassli						
Spring (<i>n</i> = 9)	3.4 (1–5)	3	1.5	1.7 (1–4)	2	0.8
Autumn (<i>n</i> = 11)	6.1 (5–9)	5	1.5	6.6 (3–10)	6	2.3
Increase spring-autumn (<i>n</i> = 9)	2.7 (0–8)	2.5	2.3	4.9 (1–9)	6	2.7
% increase	80%			287%		
St.5. Outlet Lake Atnsjøen						
Spring (<i>n</i> = 4)	8.5 (5–12)	8	2.6	9.0 (6–11)	10	2.6
Autumn (<i>n</i> = 6)	11.0 (9–11)	11	1.5	11.7 (10–16)	11.5	1.9
Increase spring-autumn (<i>n</i> = 4)	2.5 (0–10)	0.5	3.2	2.7 (0–12)	1	4.5
% increase	29%			30%		
St.6 - Sollia						
Spring (<i>n</i> = 9)	6.4 (4–9)	6	1.6	7.7 (4–14)	7	3.3
Autumn (<i>n</i> = 11)	8.2 (6–12)	8	1.7	12.0 (10–17)	12	1.2
Increase spring-autumn (<i>n</i> = 9)	1.7 (–1–8)	2	2.6	4.3 (–3–12)	5.5	4.5
% increase	27%			57%		
St.7 - River Setninga						
Spring (<i>n</i> = 9)	6.6 (3–10)	7	2.5	2.4 (1–4)	2	0.9
Autumn (<i>n</i> = 11)	7.2 (3–11)	7	1.5	7.9 (4–11)	8	2.1
Increase spring-autumn (<i>n</i> = 9)	0.6 (–2–6)	1.5	2.8	5.5 (2–10)	7	2.5
% increase	9.6%			224%		
St.8 – Solbakken						
Spring (<i>n</i> = 9)	9.3 (6–13)	8	2.5	7.1 (3–13)	5	3.6
Autumn (<i>n</i> = 11)	10.5 (8–13)	10	1.5	15.1 (12–19)	15	2.1
Increase spring-autumn (<i>n</i> = 9)	1.1 (–4–10)	1	3.7	8.0 (0–15)	9	4.4
% increase	12%			112%		

Discussion

The periphyton in River Atna represents a community typically found on riffle localities, in cold, nutrient poor rivers with low humic content and low to medium alkalinity. It may serve as a reference community for this type of river (Skuja, 1964; Backhaus, 1968; Kann, 1978; Johansson, 1982; Lindstrøm, 2000). It is a general assumption that pristine environments sup-

port greater diversity of organisms than do polluted environments. It is also assumed that streams in marginal environments (e.g. high physical disturbance, low temperature, low nutrient content) may exhibit low diversity in the absence of pollution (Wehr, 1981). This seems to apply for the upper part of the River Atna that had very low diversity. Our studies revealed considerable spatial and temporal variation in species composition and diversity. The spatial variation was

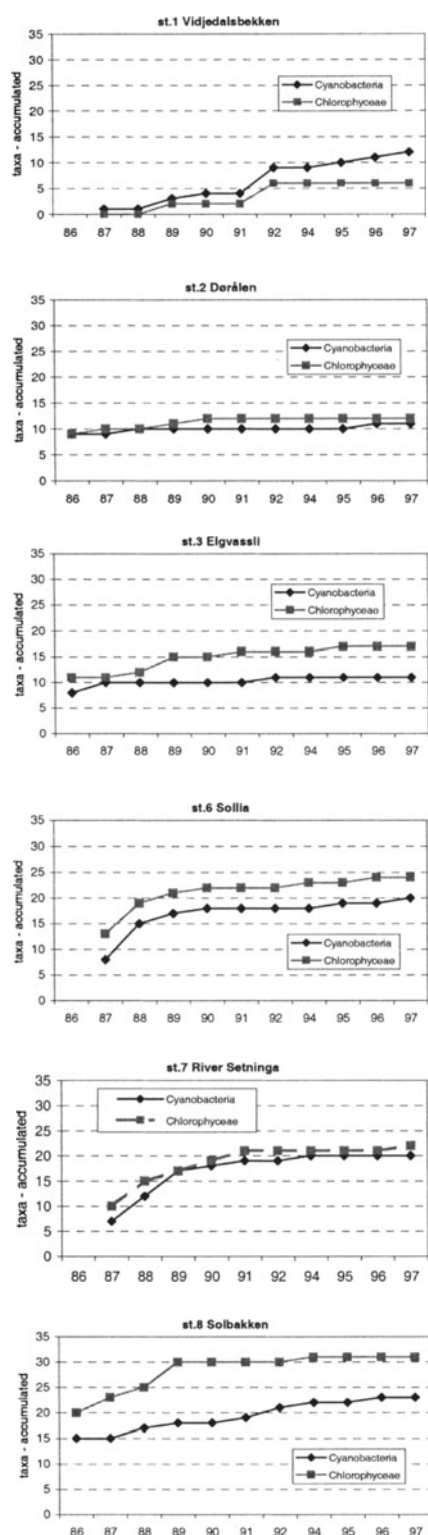


Figure 7. Accumulated number of taxa (cyanobacteria and green algae) collected in the autumn during the period 1986–97 at six sampling stations in River Atna.

Table 9. Linear regression of number of taxa (Y, cyanobacteria and green algae) versus selected environmental factors (x) in River Atna 1986–97. (cf. Fig. 8).

Factor	R^2	Regression model
Altitude	0,5265	$Y = -47,908x + 1027,8$
Growth period length	0,5875	$Y = 2,7663x + 104,15$
TOC	0,5981	$Y = 8,8277x - 2,3799$
tot-P	0,3848	$Y = 0,1697x + 2,3246$
pH	0,1024	$Y = 0,0377x + 5,89692$
Conductivity	0,0822	$Y = 0,3712x + 9,728$
Calcium	0,0562	$Y = 0,0555x + 0,8387$
Alkalinity	0,027	$Y = 0,0113x + 5,9017$

correlated with environmental gradients, illustrating how gradients within a relatively small pristine watershed may affect biota. This highlights the need for diversified knowledge about reference conditions.

The stream environment may provide a great diversity in microhabitats, e.g. local light and temperature regimes, physical disturbance and stability, substrate type, current velocity and periodic aeration (Biggs, 1996; Lake, 2000). This type of diversity was not addressed in this study, but the effects were recognisable in the field. For instance, filamentous green algae had a patchy distribution in the river. Some species grew in a zone along the riverbank that was warmed up by the sun during the day (e.g. *Microspora palustris* v. *minor*). Some grew in periodically dry areas along the riverbank (e.g. *Bulbochaete*), others in the torrents apparently directly on stones (e.g. *Klebsormidium rivulere*), or on submerged bryophytes (e.g. *Oedogonium* c.).

Longitudinal distribution

It is generally accepted in the river continuum concept, that most watercourses change character from the upper sources until they attain 'ecological maturity' further downstream (Sjörs, 1967; Margalef, 1968; Vannote et al., 1980). A river passes on its way several ecological niches containing new species that may become an integrated part of the river (Vannote et al., 1980). This change was striking in River Atna. Periphyton species composition and diversity exhibited substantial variation along the river, new species were introduced all the way down and no algae appeared as 'character species' along the entire river.

Two environmental gradients, water chemistry and water temperature (reflecting climate, all sites had

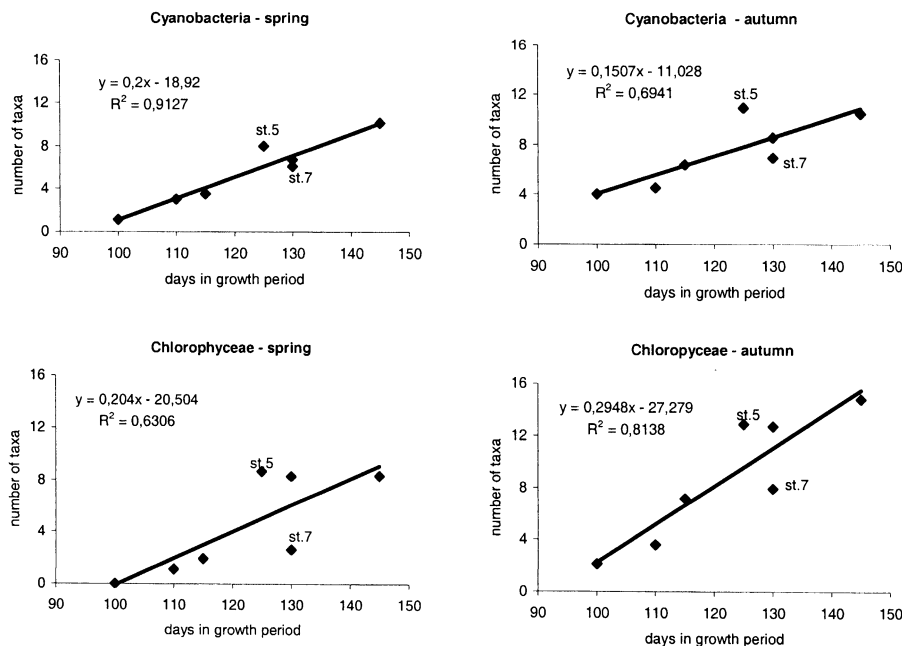


Figure 8. Scatter-plot of covariance: diversity (taxa cyanobacteria and green algae) versus days in theoretical growth period, River Atna 1986–97. R^2 of the regression line and equation are given in figure, confidence interval 95%.

sufficient insolation), were expected to be major differentiating factors. The sampling programme was designed to minimise differences in hydrological variables, and hydrology was not expected to be an important differentiating factor. All sampling sites were located in riffles with high current velocity and coarse substratum (Table 1), and all except maybe st.5 outlet of Lake Atnsjøen, were exposed to the rapid/sharp changes in discharge that may occur.

The data support the assumption that water temperature and nutrients governed species composition and diversity. It was, however, close correlation between these two gradients, and it may be difficult to intercept their relative significance. Close correlation was found between species composition and altitude (Fig. 6C), duration of the growth period (Table 6), total phosphorus (Fig. 6D) and total organic carbon (Table 6). A similar strong correlation was found between species diversity and the same environmental parameters (Fig. 8, Table 9). Species composition showed significant correlation with pH, and less strong with Ca and alkalinity (Table 6). This was somewhat contradictory to other studies that emphasise pH (and the related variables Ca and alkalinity), as the chemical variables with the strongest impact on periphyton species composition (Hill et al., 2000; Lindstrøm, 2000). Low correlation with pH and related variables may be

attributed to the cold climate and the limited nutrient supply that probably overrule other environmental variables. Little correlation was found between diversity and pH, Ca and alkalinity (Table 9). This is in agreement with other observations, pH (Ca and alkalinity) does not affect species diversity severely unless pH is below 5.0–5.5 (Lindstrøm, 1992; 2000).

The localities investigated in this programme may be classified into three to four different programme categories in terms of environmental variables and periphyton species composition and diversity:

1. The category in the upper ultra oligotrophic reaches (station 1, 2 and to some extent 3, at 1150–740 m altitude) can be characterised by cold climate (<100–120 days in growth period), extremely nutrient poor water (TOC 0.5 mg l^{-1} , tot-P $2 \mu\text{g l}^{-1}$; Table 2) and low alkalinity. Both temperature and nutrient supply are marginal, and only algae adapted to this demanding environment are able to survive. This affects species composition and curtails species diversity. This category can be distinguished by the cyanobacteria, *Chamaesiphon subglobosus*, *Phormidium* sp2, *P. autumnale* and *Scytonematopsis starmachii*, by very few green algae *Klebsormidium rivulare* and *Microspora palustris* v. *minor* (only from st.2 and down, no green algae found regularly in the up-

- per st.1 Vidjedalsbekken), and by the chrysophyte *Hydrurus foetidus*. Species diversity is low, much lower than average for 110 other fairly unpolluted river sites in Norway. Average number of taxa of green algae and cyanobacteria (autumn samples) at st.1 and st.2 was 6.1, versus 12.6 at the 110 other sites (Lindstrøm, 2000).
2. A second category (station 5 and 6; at 701 and 522 m altitude) is characterised by intermediate climate (120–140 days in growth period) and in this context intermediate nutrient content (TOC 1–1.2 mg l⁻¹, tot-P 3–4 µg l⁻¹; Table 2). It can be distinguished by the cyanobacteria *Calothrix gypsophila*, *Clastidium setigerum* and *Stigonema mamillosum* and by the green algae *Oedogonium* c., *Bulbochaete* sp., *Zygnema* a and *Z. melamosporum*. Species diversity is considerably higher than in category 1.
 3. A third category (represented by st.7 River Setninga) may be distinguished by high pH, calcium and alkalinity (pH 7.2, Ca 3.2 mg l⁻¹, alk. 180 µekv l⁻¹; Table 2) and by cold water. The length of the theoretical growth period (based on air temperature) is equal to the nearby st.6 Sollia (category 2, 130–140 days), but the *water temperature* is 1–2 °C lower (unpublished data). This is due to large deposits of snow in the catchment area of River Setninga that may contribute cold water during the whole summer. Moreover, there is no large lake upstream that stabilises the water temperature in the river (Fig. 1). This category may be distinguished by the cyanobacteria *Chamaesiphon fuscus*, *Phormidium hetropolare* and *Tolypothrix distorta*, by the green algae *Microspora amoena*, *Ulothrix zonata* and *Spirogyna lapponica* and by the red algae *Lemanea fucina*. It may also be distinguished by low diversity. It is suggested that low temperature affected diversity in particular.
 4. This category, represented by st.8, can be distinguished by a few species of green algae that only grow in the lower reaches of the river, e.g. *Spirogyna* d (*majuscula*?), and by a species diversity that is distinctly higher than average for other running water localities in Norway (Lindstrøm, 2000). It has intermediate nutrient content (TOC 1.35 mg l⁻¹, tot-P 4 µg l⁻¹; Table 2) and intermediate pH, calcium and alkalinity (pH 6.7, Ca 1.7 mg l⁻¹, and alk. 80 µekv l⁻¹). It has warmer climate than the other categories, with a growth period of 140–150 days.

A general characteristic of these categories may be given in terms of macroscopic filamentous algae, according to Israelson (1949). The community in the upper reaches is common in nutrient poor boreal and alpine rivers all over Norway (unpublished data). A suitable name in terms of filamentous algae might be *Klebshormidium Type*. Category 2 and 4 represent the typical *Zygnema Type* described from nutrient poor waters in Scandinavia by Israelson (1949). He introduced the *Vaucheria Type* as a counterpart to the *Zygnema Type*, stating that streams of the *Vaucheria Type* are characteristic of the eutrophic waters of Scandinavia. The *Vaucheria Type* was commonly found in nutrient rich areas in southern Sweden, e.g. Skåne. It does not seem to be very common in Norway, probably due to the low nutrient contents in Norwegian rivers. A substitute for the *Vaucheria Type* may be the *Ulothrix zonata Type*. The *U. zonata Type* has somewhat lower nutrient content than *Vaucheria Type*, but it is still different from the *Zygnema Type* by requiring distinctly higher conductivity (Johanson, 1982; Lindstrøm, 2000). Category 3 in River Atna may be termed the *Ulothrix zonata Type*. This type is common in Norway, in areas where the bedrock is somewhat richer than the inert types (e.g. granite, sparagmite) that dominates in the southern part of Norway.

Variations and long term trends

The periphyton at a given site revealed striking temporal stability in species composition from spring to autumn (Fig. 6A), and only a weak temporal trend was found after 12 years (Fig. 6B). Inter-annual stability was particularly high in the autumn (Fig. 5). Species diversity at a given site displayed a similar stability between years (Table 8), as well as in the long term. Only a few additional species were collected after the first three to four years (Fig. 7). Diversity at a given site did however display considerable seasonal variability (Table 8). This is in agreement with Wehr (1981) who studied the algal flora in a mountain stream in British Columbia. He found 'a remarkable persistence of the entire epilithic algal assemblage within the seasonal wax and wain of certain species'. He also found that variation in species composition and diversity correlated with temperature and chemical variables.

This remarkable temporal stability in combination with high spatial variability is probably the main reason that taxonomic periphyton observations have become an important constituent in water quality as-

sessments (Lowe & Pan, 1996). There is an increasing awareness that attached algae are ideal indicators of the health of many, if not most, aquatic ecosystems (Stevenson et al., 1996; Stevenson & Pan, 1999). If a site is studied carefully, it should be possible to revisit the site after several years to find a very similar periphyton community. This theory is supported by a Swedish example where red algae localities that had been studied around 1940 were revisited in 1999. The same species were found after 60 years (Kwandans et al., 2002). It should be possible, after some years of observations at a given site, to establish a list of expected species, in a similar way to the use of the term 'normal' for the mean values of long term observations of hydrological and meteorological data.

On the other hand, all significant changes in the periphyton community are expected to be the result of changes in the environment. In Atna, a weak, but significant temporal trend in species composition was found after 12 years. The direction of this trend was towards negative site score values (Fig. 6B). This implies that it pointed towards low-altitude sites (Fig. 6C), high tot-P values (Fig. 6D), and autumn samples (Fig. 6A). This suggests increased significance / upstream movement of species initially occurring in lowland and high nutrient sites, and/or in the autumn. This in turn indicates a change towards warmer climate / increased nutrient content. This may be related to climate change, and/or the increased nitrogen deposition that has occurred in southern Norway during the last few decades (Henriksen, 1999).

Seasonal variability appeared to be more evident for diversity (Table 8) than for species composition (Fig. 6A). It may be that seasonal variation in climate and physical disturbance in this marginal and very demanding environment affects diversity directly, while it affects species composition more incidentally/randomly (Biggs & Thomsen, 1995; Biggs, 1996; Lake, 2000). The data suggested more pronounced seasonal variation in species diversity in River Atna than in most lowland rivers studied in Norway (Lindstrøm, 2000). This is probably due to the pronounced seasonal variations and the demanding environmental conditions in River Atna.

The species diversity of green algae exhibited a more pronounced increase downstream and from spring to autumn than cyanobacteria (Table 6). This seems to be a general rule in running waters in Norway (Lindstrøm, 2000), and indicates an increased significance of green algae in relation to cyanobacteria downstream, and in relation to higher temperatures.

If green algae are more closely related to changes in temperature than cyanobacteria, they may provide better information about the impacts of climate change, particularly in high altitude areas.

Development of methods

Common qualitative methods (Jarlman et al., 1996; Kelly et al., 1998) seemed suitable to reflect periphyton species composition and diversity. Proper taxonomic knowledge is however a prerequisite for this type of work. A relatively simple parameter, the number of taxa per sample of two taxonomic groups (cyanobacteria and green algae), provided relevant data on species diversity. Comprehensive analyses, including complex index calculations, did not seem necessary to address diversity. This agrees with the statement of Wilson (1997) 'The key to the effective analysis of biodiversity is the precise definition of each level of organisation when it is being addressed'.

Differences between years in species composition and diversity were surprisingly small and it may seem that only a few years of observations are sufficient to provide a reliable general characteristic of a given locality. This is in contrast to the abundance data that were extremely variable, both during the growth period and between years (Lindstrøm & Johansen, in prep.).

Species composition and diversity displayed pronounced zonation along the watercourse. The high impact of the spatial factor must be taken into consideration when a reference site is selected. This seems to be particularly important in marginal environments where natural nutrient supply and climate may overrule other factors. The decrease in inter-annual similarity at st.7 River Setninga after the station was moved indicates that minor physical differences at the sampling site may affect species composition and diversity. It is therefore not advisable to change the sampling site during the observation period. If the objective is to map a majority of the natural zonations and differences that pristine watercourses may support, then a fairly high number of sampling sites may be required.

Considerable seasonal variation in diversity illustrates the importance of sampling time. Substantial changes in diversity, and to some extent species composition, may take place within a short growth period. Samples from the same site showed more variation in species composition and diversity in spring than autumn. This suggests that the periphyton community

was in a more stable state, and provided more reliable information in the autumn than in spring.

Data based on regular chemical observations were only available from four of the seven stations, and variables commonly used to characterise the significance of water quality on periphyton, e.g. TOC and tot-P, were not measured regularly. Covariance between periphyton and chemical conditions is expected to be closer than this study demonstrated, if relevant chemical variables are measured regularly at all sampling stations and data made available in detail.

Acknowledgements

This study was financed by the Norwegian State Pollution Authority (SFT), the Norwegian Directorate for Nature Management (DN) and the Norwegian Institute for Water Research (NIVA). The authors thank all three institutions. We also acknowledge the help of our colleague Randi Romstad who carefully analysed and identified many periphyton samples. Other colleagues at NIVA are thanked for field assistance. Dr Odd Terje Sandlund provided helpful comments on the final draft of the manuscript. Finally we thank Kaare Aagaard who promoted the idea of a publication that summarises the observations conducted in River Atna.

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Studies of aquatic insects in the Atna River 1987–2002

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Key words: zoobenthos, RCC, bio-monitoring, long term studies, altitudinal zonation

Abstract

River Atna is situated in south-eastern Norway and stretches from approx. 1400 m a.s.l. in the Rondane Mountains, through Lake Atnsjøen, at 701 m a.s.l.; to the confluence with River Glomma at 338 m a.s.l. The catchment area is 1323 km², oligotrophic and very susceptible to acid precipitation. The river water is very poor in nutrients and ions, and pH varies from 5.0 to 7.2. Samples were taken each year from 1987 to 2002 at three to five localities from 1280 to 380 m a.s.l. Insect larvae were collected by Surber sampling and by kick sampling. Malaise traps were used to collect adults of Plecoptera, Trichoptera, Chironomidae and Limoniidae. A total of 16 taxa of Ephemeroptera, 24 taxa of Plecoptera, 39 taxa of Trichoptera, 125 taxa of Chironomidae and 52 taxa of Limoniidae, were identified. Our results from Atna provide some support for a zonation of the river based on zoobenthos. The occurrence and abundance of functional groups among the Plecoptera, Trichoptera, and Chironomidae are discussed in relation to the River Continuum Concept (RCC). Our conclusion is that grazers dominate in the zoobenthos in streams in the treeless alpine region in Norway. Natural lakes, which occur in most watercourses in Norway, appear to cause a disturbance in relation to the original RCC concept, as the zoobenthos community in and below the lake outlet is dominated by collectors (filter feeders). The pattern found in the Atna watercourse is probably a general pattern for a northern watercourse in the Holarctic, where the glacial periods created lakes in most watercourses. The results of the long term sampling in Atna are discussed in relation to the practicalities and the cost-benefit of zoobenthos in efficient bio-monitoring in rivers.

Introduction

Longitudinal distribution and community structure of invertebrates in rivers have been discussed in several papers over the last 40 to 50 years. The earliest papers were descriptive and focused mainly on the distribution of benthic communities (Müller, 1953; Illies, 1956, 1961; Illies & Botosaneanu, 1963). However, Webster (1975) pointed out that nutrients in a stream do not cycle in place, but are transported downstream as they complete a cycle; this coupling of transport and energy cycling was described as a 'spiralling' effect. This idea was further developed by Vannote et al. (1980) who introduced the River Continuum Concept (RCC). RCC takes into consideration not only the

species composition, but also the production, respiration and feeding habits of the species, providing a more holistic and dynamic view of the running water ecosystem. The RCC classifies the zoobenthos in functional groups based on their feeding habits, i.e. grazers, shredders, collectors (filter feeders), and predators. Vannote et al. (1980) postulated a gradual change in community structure from the source of the river to its end in the ocean. In their study, the river source was in forest, i.e. heavily shaded, and they demonstrated a gradual change in the production/respiration ratio along the river. At the source, respiration was larger than production. Some distance downstream, production increased to become larger than respiration, while even further downstream res-

piration again became larger than production. Other authors, e.g., Statzner & Higler (1986) and Statzner (1987) focused on the stream hydraulics as an important factor governing the distribution of species. Townsend (1989) introduced the patch dynamics concept of stream community organization, stressing the importance of competition, succession, predation, grazing and disturbance.

Norway (and Scandinavia) has been classified into several biotic zones based on terrestrial vegetation (Moen, 1999). Subsequently, the vertical zonation of Plecoptera and Trichoptera in rivers in relation to the zonation in adjacent terrestrial ecosystems was discussed by Lillehammer (1974) and Solem (1985). In this study we have collected zoobenthos from the river Atna, which runs through several vegetation zones (Table 1), in order to analyse the spatial and temporal changes in the community structure of Ephemeroptera, Plecoptera and Trichoptera. We have also included data on the species composition of Diptera families Chironomidae and Limoniidae.

The objectives of the study were:

- (1) to document the species inhabiting the river;
- (2) to describe the longitudinal zonation in the aquatic insect communities and relate the aquatic fauna to the terrestrial biotic zonation;
- (3) to discuss the occurrence and dominance of functional groups in the different biotic zones in relation to the RCC concept; and
- (4) to evaluate the monitoring value of a low effort long term study.

Methods

Insect larvae were collected by Surber sampling and by kick sampling. The net meshes in the 0.1 m² Surber sampler and kick sampling net were 0.5 mm. Caddis larvae (Trichoptera) were also handpicked, mostly in the upper parts of the river system. Mayflies (Ephemeroptera) are best caught with the kick sample method (Engblom, 1996). The use of the Surber sampler is probably one of the reasons for a relatively low specimen number in the samples. A careful use of the Surber method has nevertheless been shown to increase the number of rare taxa collected on heterogeneous substrates, while the number of specimens is lower in Surber samples compared to kick samples (Storey et al., 1991).

Malaise traps were used to collect adults of stoneflies (Plecoptera), caddis flies, limonids and chironomids.

This adds information on species occurrence to facilitate community analyses and to reveal distribution patterns. One argument against sampling with Malaise traps for community analyses, is that species may fly in from other habitats than the one targeted by the sampling. However, Solem (1985) tested the validity of the Trichoptera collections in Malaise traps against emergence traps in the stream Raubekken, Dovrefjell, and concluded that Malaise trap collections are adequate for community analyses. Although the Malaise trap will always capture a few specimens of species that do not belong to the nearby community, these specimens are so few that they will not seriously disturb the general community analyses. An obvious advantage of Malaise traps is that they may sample continuously during the whole flying season, from late June, through July, August and September. During our sampling programme, the traps were emptied every week and the animals were conserved in ethanol.

Study area and sampling sites

River Atna is situated in southeastern Norway and originates in the Rondane Mountains well above the tree line, which is at 1100 m a.s.l. The river is 97 km long, and Lake Atnsjøen, at 701 m a.s.l., is situated in the middle of the water course. Atna joins River Glomma at 338 m a.s.l. Our sampling sites are situated between approximately 62° N, 9° 45' E and 61° 45' N, 10° 45' E (Fig. 1). Surber samples were taken each year from 1987 to 2002 at three localities; Dørålseter, Vollen, and Solbakken, and covered a nearly 80 km stretch of the river. Surber samples have also been taken in some of the later years at Skranglehaugan (Table 1). The material of benthic insect larvae from these samples has been identified mostly to the species or genera level for the groups Plecoptera, Ephemeroptera and Trichoptera.

Material of adult insects was collected with Malaise traps at Vidjedalsbekken Skranglehaugan, Dørålseter, Vollen, the outlet of Lake Atnsjøen and Solbakken (Table 1). Imagines of Trichoptera and Plecoptera were identified from all these localities, while imagines of Ephemeroptera and males of Chironomidae and Limoniidae were identified from Vidjedalsbekken, Skranglehaugan, Dørålseter, Vollen and Solbakken.

The water in the river is very poor in nutrients and ions, and pH varies from 5.0 to 7.2 (cf. Lindstrøm et al., 2004). The catchment area is 1323 km², oli-

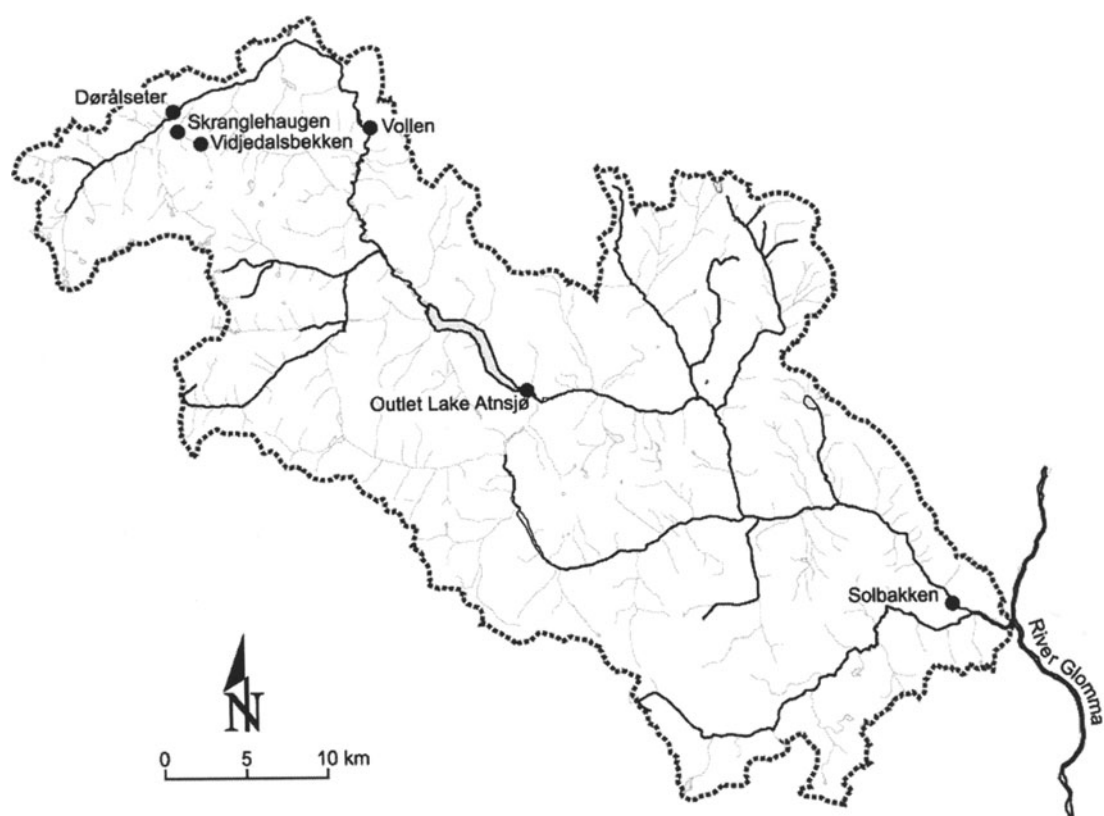


Figure 1. Map of the Atna watershed with sampling localities (cf. Table 1).

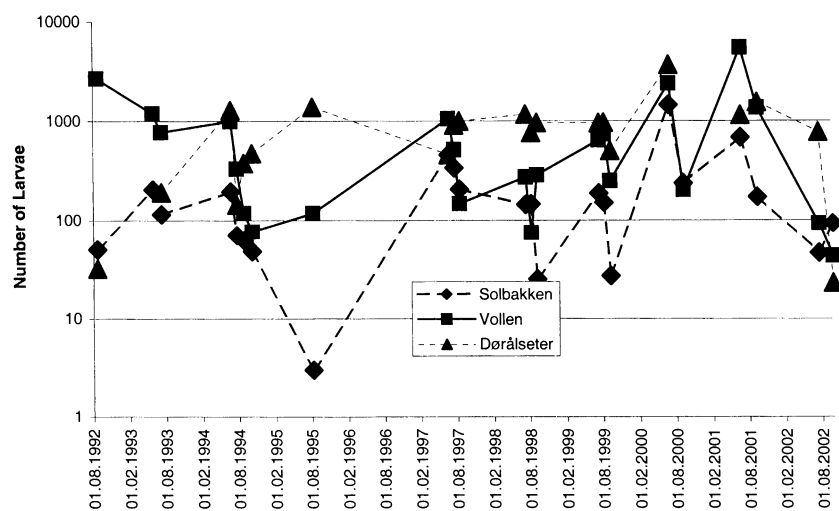


Figure 2. Number of Chironomid larvae in the Surber samples during the period 1992 to 2002.

Table 1. Sampling sites with altitude, vegetation type, vegetation zone and -section according to Moen (1999), and zoobenthos sampling program.

Station	Altitude (m a.s.l)	Vegetation type	Vegetation zones	Vegetation sections	Surber samples	Malaise traps
Vidjedals-bekken	1280	Treeless area	Alpine	Continental to oceanic	–	1986 and 1987
Skrangle-haugan	1120	Birch woodland belt	Northern boreal	Continental to oceanic	1997–2002	1986 and 1987
Dørålseter	1060	Birch woodland belt	Northern boreal	Continental to oceanic	1987–2002*	1986 and 1987
Vollen	710	Coniferous area	Northern boreal	Slightly continental	1987–2002*	1986
Atnsjøen	700	Coniferous area	Northern boreal	Slightly continental	–	1986
Solbakken	380	Coniferous area	Middle boreal	Slightly continental	1987–2002*	1986

*The material from 1996 was lost in an accident.

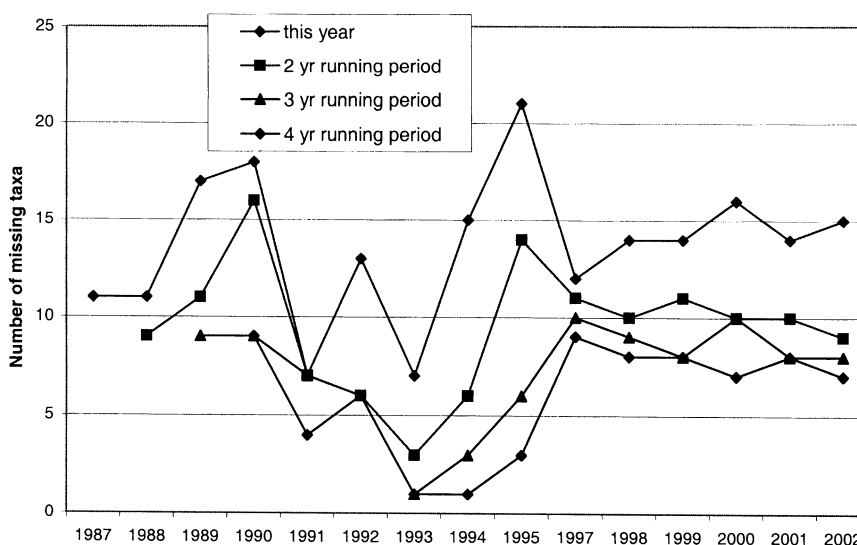


Figure 3. Number of missing taxa in the Surber samples at Solbakken for each year and running periods for the last 2, 3 and 4 years.

gotrophic and very susceptible to acid precipitation (Blakar et al., 1997). The water temperature in the lower part of the river, below the lake, may reach 20 °C during summer, with mean temperatures in June to August at 10–12 °C. Upstream of Lake Atnsjøen, the water temperature may reach 10 °C only for short periods during summer. At Vidjedalsbekken, in the subalpine birch woodland belt, maximum water temperature may reach 7–8 °C during summer, with mean temperatures during July and August of 4–6 °C. At Dørålseter a little further downstream, maximum summer temperatures may reach 10–11 °C. The increase in water temperatures during spring occurs nearly two months later at Vidjedalsbekken than at Solbakken, and there is a corresponding difference in summer temperature of 6 °C (Tvede, 2004). River Atna and its tributaries, including Vidjedalsbekken, is unregulated, and only to a very limited extent influenced by human

activities. No part of the tributary or river is significantly shaded by terrestrial vegetation. Consequently, the light conditions are very good for periphyton growth on the substratum.

Results

Distribution and abundance of Ephemeroptera

A total of 16 taxa of mayflies were identified in the material collected during the years 1986–2002 (Table 2). This includes an unidentified Leptophlebiidae collected at Solbakken. *Baetis rhodani* is by far the most common species in the river. In fact 30 000 individuals out of a total of 36 000 collected mayfly nymphs belonged to this species, which is by far Norway's most common running water mayfly species. *B. rhodani*

Table 2. Distribution of Ephemeroptera species in the river Atna. Species records at each of the localities quantified as very abundant or abundant (xxxx or xxx), less abundant (xx) or rare (x). An *i* indicates that the species are identified from imago.

Locality	Skranglehaugan	Dørålseter	Vollen	Solbakken
<i>Baetis lapponicus</i>	x	x		x
<i>Baetis rhodani</i>	xx	xxxx	xxxx	xxxx
<i>Ephemerella aurivillii</i>		x	xxx	xxxx
<i>Heptagenia joernensis</i>		x	xx	xxx
<i>Baetis muticus</i>		x	x	xxx
<i>Baetis fuscatus/scambus</i>		x	x	xxxx
<i>Ameletus inopinatus</i>		x	xx	xx
<i>Siphonurus lacustris</i>		<i>i</i>	<i>i</i>	<i>i</i>
<i>Baetis subalpinus</i>			xx	xxx
<i>Heptagenia dalecarlica</i>			x	xxx
<i>Siphonurus aestivalis</i>			x	
<i>Baetis scambus</i>				xx
<i>Ephemerella mucronata</i>				xx
<i>Heptagenia sulphurea</i>				x
<i>Leptophlebiidae</i>				x
<i>Parameletus chelififer</i> *				
Number of species	2	8	10	14

* Imago found in a Malaise trap at the outlet of Lake Atnsjøen.

is a collector-gatherer and grazer (scraper) (Bækken, 1981; Elliott et al., 1988).

At the site Skranglehaugan, 1120 m a.s.l., only nymphs of *B. rhodani* and *B. lapponicus* were recorded in the Surber and kick samples. At this elevation mayflies are at their extreme altitudinal limit in Norway. The third species of this genus known from high altitudes, *B. subalpinus*, was not found at the two high altitude sites (Vidjedalsbekken, Skranglehaugan) in Atna. This is somewhat surprising, since this species is characterised as a northern, high altitude species in Norway (Nøst et al., 1986).

Eight species of Ephemeroptera were found at Dørålseter, which is situated in the birch woodland belt (1060 m a.s.l.) (Table 2). The site with most mayfly species was Solbakken in the middle boreal zone, where 14 species were recorded. At this site, *Baetis fuscatus/scambus* were caught in considerable numbers. Nymphs of the two species may not be easily separated (Elliott et al., 1988). However, as no *B. fuscatus* imagines has yet been recorded in Atna, it appears reasonable that the nymphs collected mainly were *B. scambus*. The two species *Heptagenia dalecarlica* and *H. joernensis* were present in large numbers at Solbakken, while only one specimen of *H. sulphurea* was caught during all the sampling years. All mayfly species recorded in Atna during our sampling period

(1986–2002) are common in Norway, except the species *Parameletus chelififer* that was found in a Malaise trap at the outlet of Atnsjøen. This species is missing in large parts of western and northern Norway, although it is not formally listed as rare or uncommon. *Ameletus inopinatus* has not previously been recorded from the area (Brittain et al., 1996).

Distribution and abundance of Plecoptera

The stonefly fauna must be considered well documented through this investigation. In our material we identified 24 of the 28 species previously recorded in the region (Table 3; Aagaard et al., 2002). Stoneflies generally prefer cold, clean, running waters, and a few species occur at all altitudes in all parts of Norway. The four species not recorded in this study is either a lake dweller (*Diura bicaudata*), or they are species with a distribution mainly restricted to lowland areas. (*Dinocras cephalotes* occurs in brooks and large rivers, *Isoperla difformis* has a wide, but sparse distribution, and *Isogenus nubecula* has a southern and eastern distribution in Scandinavia and is therefore rare in Norway).

A total of 7048 stonefly nymphs were recorded in the Surber samples. *Capnia atra* was the most abundant species with a maximum at Dørålseter, while

Table 3. Distribution of Plecoptera species in the river Atna. Species records at each of the localities quantified as very abundant or abundant (xxxx or xxx), less abundant (xx) or rare (x). An *i* indicates that the species are identified from imago.

Locality	Skranglehaugan	Dørålseter	Vollen	Solbakken
<i>Capnia bifrons</i>	<i>i</i>			
<i>Arcynopteryx compacta</i>	xx	xx		
<i>Brachyptera risi</i>	x	xxx	xx	
<i>Nemoura cinerea</i>	x	xx	<i>i</i>	<i>i</i>
<i>Capnia atra</i>	xx	xxxx	xxx	x
<i>Protonemura meyeri</i>	xx	xxx	xx	x
<i>Nemurella pictetii</i>	xx	xx	x	x
<i>Amphinemura borealis</i>	x	x	xx	xxx
<i>Diura nanseni</i>	x	x	xxx	xxx
<i>Isoperla obscura</i>	x	x	xxx	x
<i>Isoperla grammatica</i>	x	<i>i</i>	xxx	x
<i>Leuctra fusca</i>	<i>i</i>	x	x	xx
<i>Capnia pygmaea</i>	<i>i</i>	<i>i</i>	<i>i</i>	<i>i</i>
<i>Amphinemura standfussi</i>		<i>i</i>	<i>i</i>	
<i>Leuctra digitata</i>		xx	x	xx
<i>Leuctra nigra</i>		x	xx	x
<i>Leuctra hippopus</i>		x	xx	x
<i>Taeniopteryx nebulosa</i>		x	xxx	xx
<i>Nemoura avicularis</i>			x	<i>i</i>
<i>Capnopsis schilleri</i>			x	
<i>Siphonoperla burmeisteri</i>			x	xx
<i>Amphinemura sulcicollis</i>			xx	x
<i>Nemoura flexuosa</i>				<i>i</i>
<i>Xanthoperla apicalis</i>				<i>i</i>
Number of species	13	17	20	19

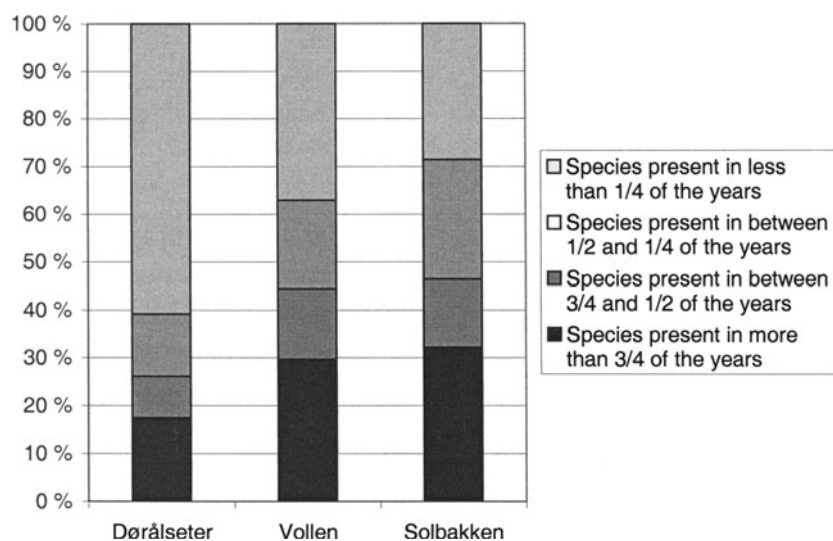


Figure 4. Number of species with different frequency of occurrence in the annual Surber samples at the three localities Dørålseter, Vollen and Solbakken in Atna, 1986–1998.

Diura nanseni dominated the samples from Vollen and Solbakken. No species were recorded in Malaise traps at Vidjedalsbekken, 1290 m a.s.l. in the midalpine zone. In the birch woodland belt (Skranglehaugan and Dørålseter) 17 species were found, and the fauna was dominated by *Capnia atra*, *Brachyptera risi* and *Protonemura meyeri*. *B. risi* is a grazer (scraper) on periphyton in streams. *P. meyeri* is a grazer and shredder. All the 24 species, except *Arcynopteryx compacta*, were collected in the boreal zone. *A. compacta* is an alpine species, and was only found at the two uppermost sites, Dørålseter and Skranglehaugan.

Capnia species dominated at high altitudes. This genus includes three species in Atna, *C. atra*, *C. bifrons* and *C. pygmaea*. *C. atra* is the dominating species, according to our Malaise trap catches along the river. Other species caught in large numbers are *Amphinemura borealis*, *Leuctra fusca*, *Isoperla obscura* and *Taeniopteryx nebulosa*, all common species in Norway.

Distribution and abundance of Trichoptera

A total of 39 species of caddis flies were identified in our material from Vidjedalsbekken and the river Atna. One species was collected in the alpine zone, 14 species in the birch woodland belt, and 38 species in the boreal zone (Table 4). At the high altitude site Vidjedalsbekken, 1280 m a.s.l., the parthenogenetic *Apatania zonella* was the only caddis fly caught in the Malaise traps. At Skranglehaugan, the collecting site in the upper part of the birch woodland belt, the Scandinavian endemic, *Apatania hispida*, was the dominant species with more than 90% of the total number of individuals. In the lower part of the birch woodland belt at Dørålseter, 14 species were collected, with three species fairly equally represented. *A. hispida*, *Potamophylax cingulatus* and *Ecclisopteryx dalecarlica* each made up between 20 and 31% of the catches.

There are no conspicuous changes in the caddis fauna at the collecting sites from Dørålseter, at 1060 m a.s.l., and downstream to Vollen, at 710 m (Table 4). However, an obvious change in the caddis fly community was found at the outlet of Lake Atnsjøen, where the collector or filter feeder (i.e. net-spinning caddis) *Polycentropus flavomaculatus* constituted more than 70% of the total number of individuals. The highest number of caddis fly species, 34, was recorded at the site Solbakken in the mid-boreal zone, at 380 m elevation.

Distribution and abundance of Limoniidae

We captured 52 taxa of Limoniidae during this study (Table 5). This family includes both aquatic and terrestrial species. Six species were recorded in the alpine zone, 21 in the birch woodland belt, and 41 species in the boreal zone (Solem & Mendel, 1989). At Vidjedalsbekken, in the birch woodland belt, the dominant species in the Malaise traps, *Phyllolabis macrura*, is a terrestrial species, but the *Orimarga* and *Ormosia* species are aquatic. They are probably shredders and collectors/gatherers, respectively. *Dicranota guerini* is a predator, and dominates (about 64%) the Limoniidae fauna in the birch woodland belt. *Ormosia fascipennis*, *Rhaphidolabis exclusa* and *Molophilus flavus* are subdominant here.

Distribution and abundance of Chironomidae

A total of 125 species of Chironomidae were found in the Malaise trap samples from the five localities. Twentyeight species were recorded at Vidjedalsbekken, 54 at Skranglehaugan, 62 at Dørålseter, 54 at Vollen, and 52 species at Solbakken. Due to the traps' positions at the different sampling sites, the samples are more representative for the stream fauna at the alpine sites than at Vollen and Solbakken. At the boreal sites, a larger number of the species caught are most probably 'tourists' from other habitats. However, the impression of a clear zonation of the species composition is not seriously effected by this problem.

The chironomids are always an important component of the fauna in alpine streams. Although Vidjedalsbekken is not glacier feed, it shares many similarities with such brooks, which is reflected in the chironomid fauna. A chironomid community of ten *Diamesa* species and several species of *Pseudodiamesa*, *Tokunagaia*, *Tvetenia*, *Eukiefferiella* and *Chaetocladius* characterizes the three uppermost alpine localities. A total of 33 species were only captured in this region (Table 6). While only five species were found at both Vidjedalsbekken and Solbakken, 39 other species occurred both in the alpine and boreal part of the river (Table 7). A surprisingly high number of species, 48 in all, were captured only in the lower part of the river at Vollen or Solbakken (Table 8). The common occurrence of 'tourist species' originating from other habitats is most probably the main reason for this. The material of Chironomidae larvae taken in the Surber samples was not identified below the family level in this study. The number of individuals in five Surber samples was mostly found to be between 100 and

Table 4. Distribution of Trichoptera species in the river Atna. Species records at each of the localities quantified as very abundant or abundant (xxxx or xxx), less abundant (xx) or rare (x). An *i* indicates that the species are identified from imago.

Locality	Skranglehaugan	Dørålseter	Vollen	Solbakken
<i>Potamophylax cingulatus</i>	x	xx	x	
<i>Chaetopteryx villosa</i>	x	x	x	
<i>Halesus digitatus</i>		x	x	
<i>Apatania hispida</i>	xx	xx		
<i>Apatania zonella</i>	xx	xxx	xx	xx
<i>Apatania muliebris</i>	xx	xx	xx	xx
<i>Limnephilus coenosus</i>	x	x	x	x
<i>Oxyethira flavicornis</i>		x		x
<i>Ecclisopteryx dalecarlica</i>	x	xx	xxx	x
<i>Potamophylax latipennis</i>	xx	x	x	x
<i>Lepidostoma hirtum</i>	xx	xx		xxx
<i>Apatania stigmatella</i>	xx	xx	xx	xx
<i>Glossosoma spp.(intermedia)</i>	x		xx	xx
<i>Rhyacophila nubila</i>	x	xx	xxx	xxx
<i>Arctopsyche ladogensis</i>		x		xxx
<i>Philopotamus montanus</i>	x			x
<i>Polycentropus flavomaculatus</i>			x	xxx
<i>Micropterna sequax</i>			x	x
<i>Annitella obscurata</i>			xx	x
<i>Halesus radiatus</i>			x	
<i>Ceratopsyche nevae</i>				xx
<i>Micrasema nigrum</i>				<i>i</i>
<i>Micrasema gelidum</i>				<i>i</i>
<i>Hydroptila simulans</i>				<i>i</i>
<i>Hydroptila forcipata</i>				<i>i</i>
<i>Sericostoma personatum</i>				xx
<i>Hydropsyche pellucidula</i>				x
<i>Hydroptila tineoides</i>				x
<i>Ceraclea spp.</i>				x
<i>Psychomyia pusilla</i>				x
<i>Athripsodes commutatus</i>				x
<i>Hydropsyche siltalai</i>				x
<i>Hydropsyche silfvenii</i>				x
<i>Apatania wallengreni</i>				x
<i>Phacopteryx brevipennis</i>				x
<i>Ithythricia lamellaris</i>				x
<i>Glossosoma conformis</i>				x
<i>Agapetus ochripes</i>				x
<i>Silo pallipes</i>				x
Number of species	13	14	15	34

Table 5. Distribution of Limonidae species found only at the localities in the river Atna. Species recorded at each of the localities quantified as very abundant (xxxx or xxx), less abundant (xx) or rare (x).

Locality	Vidjedalsbekken	Skranglehaugan	Dørålseter	Vollen	Solbakken
<i>Phyllolabis macroura</i>	xxx	x	x		
<i>Ormosia fascipennis</i>	xx	xx	x	x	x
<i>Limonia macrostigma</i>	x	x	xx	xxx	x
<i>Dicranota guerini</i>	x	xxx	xxx	x	
<i>Orimarga attenuata</i>	x				
<i>Melanolimonia caledonica</i>	x				
<i>Rhaphidolabris exclusa</i>		xx	xx	x	x
<i>Trichyphona immaculata</i>		x	x		
<i>Dicranota bimaculata</i>		x	x	x	
<i>Rhiphidia duplicata</i>		x	x	x	xx
<i>Brachylimnophila nemoralis</i>		x	x		xx
<i>Rhabdomastrix parva</i>		x	x		
<i>Symplecta hybrida</i>		x	x	x	x
<i>Gonomyia</i> sp.		x			x
<i>Paradicranota subtilis</i>		x			
<i>Paradicranota gracilipes</i>		x			
<i>Molophilus flavus</i>			xx		
<i>Euphyllidorea phaeostigma</i>			x	x	
<i>Dicranomyia incisurata</i>			x		
<i>Dicranomyia distendens</i>			x	x	
<i>Erinocopa trivialis</i>			x		
<i>Ormosia ruficauda</i>			x		
<i>Idioptera macropteryx</i>			x	x	
<i>Molophilus propinquus</i>					xx
<i>Parilisia vicina</i>				xxx	x
<i>Neolimnophila (placida?)</i>				x	x
<i>Dicranomyia halterata</i>				x	
<i>Limonia sylvicola</i>				x	x
<i>Metalimnobia zetterstedti</i>				x	x
<i>Dicranomyia terranova</i>				x	x
<i>Paradicranota robusta</i>				x	
<i>Erioptera lutea</i>				x	
<i>Phyllidorea squalens</i>				x	
<i>Erioconopa diaturna</i>				x	
<i>Dicranomyia modesta</i>					xx
<i>Metalimnobia 4-notata</i>					xx
<i>Dicranomyia frontalis</i>					xx
<i>Metalimnobia bifasciata</i>					x
<i>Limonia flavipes</i>					x
<i>Ula sylvatica</i>					x
<i>Limonia tripunctata</i>					x
<i>Empeda cinerascens</i>					x
<i>Euphyllidorea fulvonervosa</i>					x
<i>Archilimnophila unica</i>					x
<i>Melanolimonia morio</i>					x
<i>Ula mollissima</i>					x
<i>Ormosia staegeriana</i>					x
<i>Melanolimonia rufiventris</i>					x
<i>Dicranomyia zernyi</i>					x
<i>Dicranomyia</i> sp.					x
Number of species	6	14	18	20	29

Table 6. Distribution of Chironomidae species found only at the upper tree localities in the river Atna. Species recorded at each of the localities quantified as very abundant (xxxx or xxx), less abundant (xx) or rare (x).

	Vidjedalsbekken	Skranglehaugan	Dørålseter
<i>Bryophaenocladus inconstans</i> (Brundin, 1947)	x		
<i>Tokunagaia rectangularis</i> (Goetghebuer, 1940)	x		
<i>Pseudodiamesa nivos</i> (Goetghebuer, 1928)	xx	xx	
<i>Chaetocladius laminatus</i> Brundin, 1947	x	xx	xx
<i>Diamesa incallida</i> (Walker, 1856)	x	xx	x
<i>Diamesa gregsoni</i> Edwards, 1933	xx	x	x
<i>Eukiefferiella</i> spp.	x		x
<i>Chaetocladius dissipatus</i> (Edwards, 1929)	xx		xx
<i>Limnophyes brachytomus</i> (Kieffer, 1922)	x	xx	x
<i>Parametrioctenus</i> sp.		x	
<i>Tokunagaia scutellata</i> (Brundin, 1956)		x	
<i>Eukiefferiella dittemari</i> Lehmann, 1972		x	
<i>Tvetenia bavarica</i> (Goetghebuer, 1934)		xx	
<i>Thienemanniella</i> indet.		xxx	xxxx
<i>Chaetocladius piger</i> (Goetghebuer, 1913)		xx	xxxx
<i>Rheocricotopus effusus</i> (Walker, 1856)		xx	xx
<i>Krenosmittia camptophleps</i> (Edwards, 1929)		xx	xx
<i>Tokunagaia parexcellens</i> Tuiskunen, 1986		xxx	xx
<i>Parochlus kiefferi</i> (Garrett, 1925)		xx	xx
<i>Pseudodiamesa branickii</i> (Nowicki, 1873)		xx	x
<i>Corynoneura lobata</i> Edwards, 1924		x	x
<i>Smittia edwardsi</i> Goetghebuer, 1932		x	x
<i>Rheocricotopus chapmani</i> (Edwards, 1935)		x	x
<i>Limnophyes aagaardi</i> Sæther, 1990			x
<i>Natarsia punctata</i> (Meigen, 1804)			x
<i>Prodiamesa olivacea</i> (Meigen, 1818)			x
<i>Chaetocladius grandilobus</i> Brundin, 1956			x
<i>Corynoneura</i> indet.			x
<i>Micropsectra boralis</i> (Kieffer, 1922)			x
<i>Protanypus caudatus</i> Edwards, 1924			x
<i>Chaetocladius gracilis</i> Brundin, 1956			x
<i>Chaetocladius acuminatus</i> Brundin, 1956			xx
<i>Tvetenia calvescens</i> (Edwards, 1929)			xx
Number of taxa	9	19	26

1000 at all three localities, and the annual variation is synchronic with a maximum abundance in spring. In 1995, the extreme flood in spring (Tvede, 2004) clearly influenced the samples taken in August at the lower sampling sites (Fig. 2). At this date, the abundance at Dørålseter was normal, while the results from Solbakken showed the lowest number of chironomid larvae recorded during the ten year period. The effect of the flood was also seen in the low number of other insect groups this year.

Discussion

Zonation of the benthic communities

Because most Norwegian rivers run through a considerable altitudinal gradient over a relatively short distance, the question of biological zonation have been extensively discussed for several groups of organisms. Lillehammer's (1974) studies of Plecoptera included a variety of localities with different environmental conditions and species composition. He did not, however, find it feasible to establish a Plecoptera-based classi-

Table 7. Distribution of Chironomidae species found at five or four localities in the river Atna. Species recorded at each of the localities quantified as very abundant (xxxx or xxx), less abundant (xx) or rare (x).

Locality	Vidjedalsbekken	Skranglehaugan	Dørålseter	Vollen	Solbakken
<i>Eukiefferiella claripennis</i> (Lundbeck, 1898)	x	xxx	xxxx	xx	
<i>Diamesa bertrami</i> Edwards, 1935	xx	xxx	xxxx	xx	
<i>Orthocladius</i> (<i>Euorthocladius</i>) <i>saxosus</i> (Tokunaga, 1939)	x	xxx	x	xx	
<i>Eukiefferiella brevicealcar</i> (Kieffer, 1911)	x	x	x	x	
<i>Diamesa hyperborea</i> Holmgren, 1869	xx	xxx	xx	x	
<i>Eukiefferiella devonica</i> (Edwards, 1929)	x	xx	x	x	
<i>Chaetocladius suecicus</i> (Kieffer, 1916)	x	xx	xxxx	x	
<i>Diamesa lindrothi</i> Goetghebuer, 1931	xxx	xxx	xx	x	
<i>Diamesa latitarsis</i> (Goetghebuer, 1921)	xx	xxx	xxxx	x	
<i>Eukiefferiella minor</i> (Edwards, 1929)	xx	x	xxx	x	
<i>Orthocladius</i> (<i>Eudactylocladius</i>) <i>mixtus</i> (Holmgren, 1869)	xx	xx	x	x	
<i>Diamesa bohemani</i> Goetghebuer, 1932	xx	xx	xx	x	
<i>Limnophyes bidumus</i> Sæther, 1990	x	x	x	x	
<i>Limnophyes minimus</i> (Meigen, 1818)	x		x	x	
<i>Pseudosmittia recta</i> (Edwards, 1929)		x		x	
<i>Chironomus</i> (<i>Chironomus</i>) <i>longistylus</i> Goetghebuer, 1921		x		xx	
<i>Limnophyes natalensis</i> (Kieffer, 1914)		x		x	
<i>Limnophyes pumilio</i> (Holmgren, 1869)		x		xx	
<i>Paratrichocladius skirwithensis</i> (Edwards, 1929)		x	xx	x	
<i>Trichotanytus posticalis</i> (Lundbeck, 1898)		x	x	x	
<i>Diamesa serratosioi</i> Willassen, 1985	x	xxxx	xxxx	xxx	x
<i>Diamesa tonsa</i> (Walker, 1856)	x	xxx	xx	xx	x
<i>Bryophaenocladius nitidicollis</i> (Goetghebuer, 1913)	x				x
<i>Diamesa aberrata</i> Lundbeck, 1889	xx	xxx	xx		x
<i>Gymnometriocnemus volitans</i> (Goetghebuer, 1940)	xx	xx	x		x
<i>Orthocladius</i> (<i>Euorthocladius</i>) <i>thienemanni</i> Kieffer, 1906		xxx	x	x	x
<i>Micropsectra groenlandica</i> Andersen, 1937		xxx	xx	x	x
<i>Micropsectra lacustris</i> Säwedäl, 1975		xx		x	x
<i>Metriocnemus</i> indet.		xx	x		x
<i>Orthocladius</i> (<i>Orthocladius</i>) <i>frigidus</i> (Zetterstedt, 1838)		xx	x	x	x
<i>Limnophyes asquamatus</i> Andersen, 1935		xx		x	x
<i>Bryophaenocladius</i> indet.		x			x
<i>Parametriocnemus stylatus</i> (Kieffer, 1924)		x	xx		x
<i>Limnophyes edwardsi</i> Sæther, 1990		x	x	x	x
<i>Psectrocladius</i> (<i>Psectrocladius</i>) indet.		x	x	x	x
<i>Cricotopus</i> (<i>Isocladius</i>) indet.		x	x		xx
<i>Parapsectra nana</i> (Meigen, 1818)		x	x		x
<i>Heterotrissocladius marcidus</i> (Walker, 1856)			x	x	
<i>Micropsectra radialis</i> Goetghebuer, 1939			x	xx	
<i>Diplocladius cultriger</i> Kieffer, 1908			x	x	x
<i>Heterotanytarsus apicalis</i> (Kieffer, 1921)			xx		x
<i>Rheocricotopus fuscipes</i> (Kieffer, 1909)			xx		x
<i>Micropsectra atrofasciata</i> (Kieffer, 1911)			x		x
<i>Smittia</i> sp.			x		x
Number of taxa	19	35	36	32	22

Table 8. Distribution of Chironomidae species found only at the lower two localities in the river Atna. Species recorded at each of the localities quantified as very abundant (xxxx or xxx), less abundant (xx) or rare (x).

Locality	Vollen	Solbakken
<i>Thienemannimyia fusciceps</i> (Edwards, 1929)	x	
<i>Eukiefferiella ilkleyensis</i> (Edwards, 1929)	x	
<i>Tokunagaia excellens</i> (Brundin, 1956)	x	
<i>Parametriocnemus boreoalpinus</i> Gouin, 1942	x	
<i>Micropsectra notescens</i> (Walker, 1856)	x	
<i>Tanytarsus gregarius</i> Kieffer, 1909	x	
<i>Tanytarsus lestagei</i> Goetghebuer, 1922	x	
<i>Ablabesmyia monilis</i> (Linnaeus, 1758)	x	
<i>Orthocladius</i> (<i>Orthocladius</i>) indet.	x	
<i>Corynoneura edwardsi</i> Brundin, 1949	x	
<i>Saetheria reissi</i> Jackson, 1977	x	
<i>Ablabesmyia phatta</i> (Egger, 1863)	x	
<i>Odontomesa fulva</i> (Kieffer, 1919)	x	
<i>Endochironomus</i> indet.	x	
<i>Stictochironomus maculipennis</i> (Meigen, 1818)	x	
<i>Einfeldia longipes</i> (Stæger, 1839)	x	
<i>Thienemanniella majuscula</i> (Edwards, 1924)	x	
<i>Limnophyes schnelli</i> Sæther, 1990	x	
<i>Chironomus riparius</i> Meigen, 1804	xx	x
<i>Paraphaenocladius impensus impensus</i> (Walker, 1856)	x	x
<i>Procladius</i> (<i>Holotanypus</i>) indet.	x	x
<i>Smittia aterrima</i> (Meigen, 1818)	x	x
<i>Krenopelopia binotata</i> (Wiedemann, 1817)		x
<i>Macropelopia nebulosa</i> (Meigen, 1804)		x
<i>Nilotanypus dubius</i> (Meigen, 1804)		x
<i>Orthocladius decoratus</i> (Holmgren, 1869)		x
<i>Heleniella ornatcollis</i> (Edwards, 1929)		x
<i>Dicrotendipes tritonus</i> (Kieffer, 1916)		x
<i>Paracladopelma laminata</i> (Kieffer, 1921)		x
<i>Constempellina brevicosta</i> (Edwards, 1937)		x
<i>Micropsectra lindebergi</i> Säwedäl, 1976		x
<i>Micropsectra recurvata</i> Goetghebuer, 1928		x
<i>Paratanytarsus penicillatus</i> (Goetghebuer, 1928)		x
<i>Rheotanytarsus muscicola</i> Thienemann, 1929		x
<i>Tanytarsus fimbriatus</i> Reiss & Fittkau, 1971		x
<i>Potthastia longimana</i> (Kieffer, 1922)		x
<i>Pseudosmittia</i> indet.		x
<i>Demicryptochironomus vulneratus</i> (Zetterstedt, 1838)		x
<i>Rheotanytarsus ringei</i> Lehmann, 1970		x
<i>Chaetocladius perennis</i> (Meigen, 1830)		x
<i>Polypedilum albicorne</i> (Meigen, 1838)		x
<i>Metriocnemus hygropetricus</i> (Kieffer, 1912)		x
<i>Virgatanytarsus arduennensis</i> (Goetghebuer, 1922)		x
<i>Cardiocladius capucinus</i> (Zetterstedt, 1850)		x
<i>Rheopelopia maculipennis</i> (Zetterstedt, 1838)		xx
<i>Polypedilum convictum</i> (Walker, 1856)		xx
<i>Stempellinella brevis</i> (Edwards, 1929)		xx
<i>Limnophyes pentaplastus</i> (Kieffer, 1921)		x
Number of taxa	22	30

fication or zonation for Norwegian rivers similar to that developed by Illies & Botosaneanu (1963) for Central Europe.

Our results from Atna provide some support for a zonation based on zoobenthos. Both the Trichoptera genus *Apatania*, and several species of the chironomid genera *Diamesa*, *Pseudodiamesa*, *Tokunagaia*, *Tvetenia*, *Eukiefferiella* and *Chaetocladius*, are restricted to localities in or above the birch woodland belt. However, there were no typical alpine species of Ephemeroptera, and only one high mountain species of Plecoptera; *Arcynopteryx compacta*. In total, there is a zonation shift in benthic communities from the alpine and birch woodland belt area to the lower boreal zone, coinciding with the vegetation regions. The shift from the north boreal zone at Vollen to the middle boreal zone at Solbakken is more obscure. This may partly be due to the difference in dominating mesohabitats between these two localities. However, both localities belong to the boreal zone, and it should perhaps be expected that the finer classification based on terrestrial vegetation is not well reflected in the aquatic fauna. The aquatic environment is, after all, more continuous in temperature and nutrient level.

Trophic relationships and the RCC concept

The trophic relationship among the zoobenthos can be discussed based on taxa shifts of Plecoptera, Trichoptera, and Chironomidae along the watercourse. The Ephemeroptera do not provide useful data in this context because *Baetis rhodani* was the dominant species at all sampling localities. In Atna, the grazers (the stoneflies *Brachyptera risi*, *Protonemura meyeri*, and the caddis flies *Apatania hispidula* and *A. zonella*) dominated in the birch woodland belt. The reason is most probably the unshaded river channel together with low water temperature. *Protonemura meyeri* may also partly be a shredder, feeding on detritus. The Chironomidae species that inhabit the alpine zone and the birch woodland belt are either grazers or collectors. A similar pattern in the alpine zone and the birch woodland belt was found for Trichoptera also at Dovrefjell, further west in the Norwegian mountains (Table 9). In the boreal zone, shredders, represented by the stoneflies *Amphinemura sulcicollis* and *Ecdiopteryx dalecarlica* and the caddis fly *Annitella obscurata*, was the dominant functional group. In this zone, however, Lake Atnsjøen has a great influence on the occurrence of the various functional groups. At the outlet of the lake, the trichopteran collector or filter

feeder, *Polycentropus flavomaculatus*, dominates the community.

The River Continuum Concept (RCC) (Vannote et al., 1980) states that the shredders should dominate among the functional feeding groups when the source of the river is within a shaded area, e.g. in a forest. The RCC was further developed by Minshall et al. (1985), who included a treeless area (desert) at the source of the river. In this case, the different functional feeding groups (grazers, shredders, collectors, predators) constituted approximately one fourth of the community each. Our results from Atna, as well as the results reported from Dovrefjell (Solem 1985) (cfr. Table 9) differ from the pattern described both by Vannote et al. (1980) and Minshall et al. (1985). Our conclusion is that grazers dominate in the zoobenthos in streams in the treeless alpine region in Norway. The reason is most probably that the supply of dead organic material (detritus) from the heather-like riparian vegetation is restricted, while the light conditions provide a good environment for periphyton production (cf. Lindstrøm et al., 2004).

Natural lakes, which are found in most water courses in Norway, may be considered a disturbance in relation to the original RCC concept. The lake causes a shift in the stream ecosystem structure and function. The export of particulate organic matter (phyto- and zooplankton) from the lake (Sandlund 1982) changes the relationships between the functional feeding groups, as the filter feeders (i.e. the caddis fly *Polycentropus flavomaculatus*) come to dominate the aquatic insect community.

The RCC concept was intended as an universal model, but local topography must be taken into consideration when applying the concept. Lakes obviously constitute important elements in this. In Atna, there is a gradual change in the caddis fly community structure from the alpine to the boreal zone, but at the lake outlet there is a sudden and pronounced change in community dominance (Table 9). Therefore there is no obvious connection between the functional groups in the zoobenthos and the zonation in terrestrial vegetation given by Moen (1999). Still, the trophic relationships in the caddis fly communities are different in the alpine and boreal zones.

The pattern found in the Atna water course is probably a general pattern for a northern water course in the Holarctic, where the glacial periods created lakes in most water courses.

Table 9. Proportion of functional groups (in per cent) of Trichoptera in vegetation zones along Atna River and rivers in the Dovre mountains (from Solem 1999).

Functional group	Grazers	Shredders	Predators	Collectors
Atna				
Alpine zone	95	5	+	0
Birch woodland belt	70	24	5	1
Lower boreal zone	25	38	21	15
Outlet of Lake Atnsjøen	7	8	10	74
Dovre				
Alpine zone	90	10	0	0
Birch belt	10	40	40	10

The monitoring value of a low effort long term study

The aim of an efficient bio-monitoring is to detect possible impacts of human activities on a natural system with the lowest possible level of effort. However, as ecological systems are heterogeneous and variable at all spatial and temporal scales (Brown, 2003), the problem of all monitoring inventories is to distinguish between natural and human induced variation. In addition, nearly all sampling procedures introduce additional methodological uncertainties.

The composition of the zoobenthos in a stream varies in time on a seasonal as well as on an annual scale, and in space from the scale of bioregions to that of mesohabitats (Beisel et al., 1998). This long time study of benthic animals covers bioregional differences from the alpine to the boreal region. Mesohabitat variation was not considered a recordable parameter when the studies started in 1986, and such information is consequently not available. The intention was to cover seasonal variation through a sampling program of two or three sampling periods during the ice-free season. However, in some years the budget allowed only one sampling period. The quality of this long-term study is therefore strongly influenced by the project economy. The information gained on the number of species recorded in a single year (Appendices A, B, C) is of limited value. However, if the material is seen as information data covering longer time periods, a fundamental question of a biodiversity monitoring survey might be answered: Did species disappear or did the dominant species composition change during the monitoring period?

The Plecoptera and Ephemeroptera of this region are well known and it is therefore feasible to use these two groups in a methodological analysis. Few or no

additional species are expected to be found in this watercourse in the future, unless there is a considerable change in the environmental factors. The sampling program during 15 years in the lower and middle parts of the river, at Solbakken and Vollen, and 13 years in the upper part at Dørålseter, gave a total of 28, 27 and 23 known taxa, respectively, as most of the nymphs were identified to species. The uncertainty of the species identity of some small nymphs leaves us with some uncertainty considering the exact number of species recorded in each sample or year. The following considerations are therefore based on the number of *missing taxa*, i.e., species that have been recorded in the total material, but which in a particular year were not identified among larvae or present as a possible member of an unidentified larva group (Appendices A, B, C).

Several questions of relevance for monitoring programme designs could now be answered:

- What is the mean number of missing taxa for each year?
- If two, three or four years are seen together, what is then the mean number of missing taxa?
- How does the number of sampling periods in each year affect the number of missing taxa?

Number of missing taxa

The mean numbers of taxa not included in the samples for any one year were 13.7 at Solbakken, 13.9 at Vollen and 14.3 at Dørålseter. This is nearly 50% of the total recorded number of species at Vollen and Solbakken, and 62% at Dørålseter.

Combining samples from two, three, and four years, results in a substantial decrease in the number of

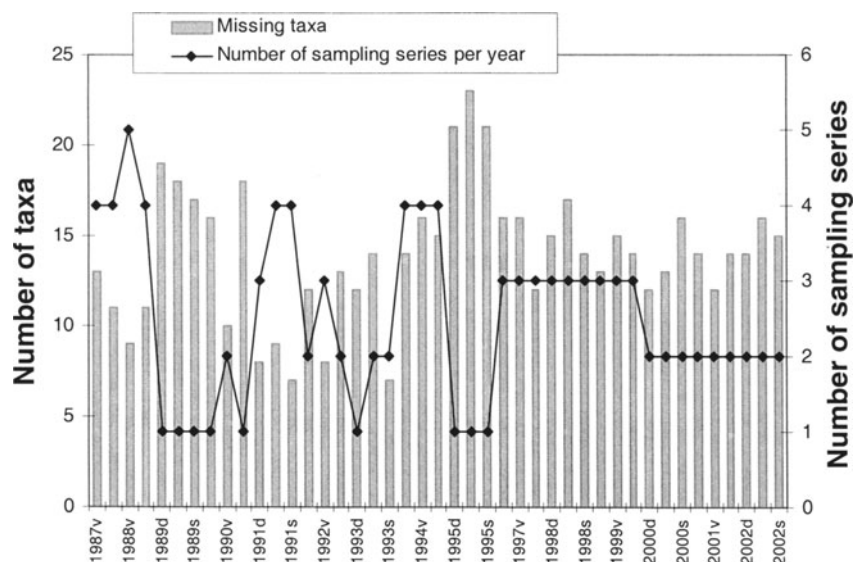


Figure 5. Number of sampling series and missing taxa at Dørålseter (d), Vollen (v) and Solbakken (s) for each year and locality.

missing taxa. At Solbakken, two, three and four years running intervals result in mean numbers of 9.5, 7.3, and 5.9 missing taxa respectively (cf. Fig. 3).

The actual results from each period show that four-year periods unveiled most of the taxa in the years before 1995. For the last 6 years, i.e. the period after 1995, the four-year running interval resulted in the relatively stable number of 7 to 9 missing taxa for each sampling period. The most dominant or abundant species were found nearly every year while more than 60% of the species at Dørålseter and about 30% of the species at Vollen and Solbakken were present in only 25% of the years (Fig. 4).

Rare species constitute a general problem in monitoring programmes. Species which occur only in a few samples are often supposed to be 'tourists' in the sense that they do not have a complete life cycle at the locality. Species with a low abundance that do not occur every year in the samples due to sampling error and/or annual variation of the population, are 'real' rare species. These species are often of great interest from a biodiversity conservation aspect. Beisel et al. (1998) found that more than 46% of the species at a given locality had both low abundance and were present in only one or a few mesohabitats on the river bed. They recommended that the sampling program was designed to include a sufficient number of mesohabitats. However, as this study indicates, species with low abundance may even then not be detected unless

the sampling effort is increased beyond all practical means.

When the results are evaluated in this way, there is no evidence for a shift in dominance or a real disappearance or extinction of any species in Atna. The most extreme results are from the year 1995 when the low number of individuals collected also resulted in a high number of missing taxa at all localities. The low number of individuals was most likely a result of the extreme spring flood in this year.

Seasonal sampling and number of missing taxa

Sampling was done one to five times per year. One sampling series per year always results in a high number of missing taxa. While two sampling series per year results in a lower number of missing taxa, there is no clear difference between two and three series per year. Four or five sampling series most often results in a low number of missing taxa, but not in all years (Fig. 5).

Monitoring of human-induced disturbance

In addition to a species by species analysis of changes in the Plecoptera and Ephemeroptera communities, there are several other methods available for describing or testing changes in community structure. Diserud & Aagaard (2002) found that the results were affected by the way the community structure was measured and that the conclusion depended heavily on the estimate

of the environmental variation. Even with a moderate expectation of environmental variation, the results could vary a great deal and still be within the limits of the expected range.

In general, monitoring a large number of rare species will always be an expensive and difficult task. Monitoring environmental changes or pollution effects, on the other hand, could be done with much lower effort through methods based on models of community structure or diversity indices. Most methods for monitoring freshwater insects are best suited for detection of pollution impacts on community structure or species composition. So far, no index of rare species, or predictive models for the occurrence of rare species, have been suggested. The methods for rare species monitoring are all based on observation of the actual species in samples, which renders these methods expensive and cumbersome.

Acknowledgements

Thanks are due to Terje Hoffstad for assistance during field work. Funding was provided by the Norwegian Research Board for Science and Technology (NTNF), the Directorate for Nature Management (DN), NTNU and NINA.

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Annex A. Plecoptera and Ephemeroptera larvae in Surber samples from Dørråseter. Species not identified but possibly present as a component of an unidentified taxon are marked by □. Species not present in the samples are indicated as missing taxa (m.t.).

Year	1989	1990	1991	1992	1993	1994	1995	1997	1998	1999	2000	2001	2002	Total	%
# sampling series per year	1	1	3	2	1	4	1	3	3	3	2	2	2	28	
<i>Baetis rhodani</i>	1	19	24	22	3	14	m.t.	m.t.	m.t.	30	10	4	1319	1446	36,88
<i>Capnia atra</i>	□	15	151	8	77	□	□	□	□	507	226	110	31	1125	28,69
<i>Protonemura meyeri</i>	m.t.	1	19	2	9	6	14	15	4	24	24	21	34	173	4,41
<i>Brachyptera risi</i>	12	m.t.	17	m.t.	6	7	m.t.	5	m.t.	m.t.	38	14	2	101	2,58
<i>Arcynopteryx compacta</i>	m.t.	6	16	4	m.t.	5	m.t.	2	3	9	3	m.t.	6	54	1,38
<i>Nemoura cinerea</i>	□	2	8	m.t.	□	m.t.	m.t.	□	□	□	3	6	20	39	0,99
<i>Nemurella pictetii</i>	m.t.	m.t.	4	m.t.	4	3	m.t.	m.t.	2	10	3	3	m.t.	29	0,74
<i>Leuctra digitata</i>	m.t.	m.t.	m.t.	m.t.	m.t.	2	m.t.	1	3	8	□	m.t.	6	20	0,51
<i>Diura nanseni</i>	m.t.	m.t.	1	m.t.	3	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	3	m.t.	7	0,18
<i>Leuctra nigra</i>	m.t.	m.t.	m.t.	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	3	1	5	0,13
<i>Heptagenia joernensis</i>	m.t.	m.t.	2	2	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	4	0,10
<i>Ephemerella aurivillii</i>	m.t.	2	m.t.	1	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	4	0,10
<i>Baetis muticus</i>	m.t.	m.t.	1	2	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	3	0,08
<i>Amphinemura borealis</i>	m.t.	m.t.	1	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	3	0,08
<i>Leuctra fusca</i>	m.t.	m.t.	m.t.	m.t.	m.t.	□	m.t.	m.t.	□	1	1	m.t.	m.t.	2	0,05
<i>Ameletus inopinatus</i>	m.t.	1	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	2	0,05
<i>Baetis lapponicus</i>	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	2	m.t.	m.t.	m.t.	2	0,05
<i>Leuctra hippopus</i>	m.t.	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	m.t.	2	0,05
<i>Isoperla obscura</i>	m.t.	m.t.	m.t.	□	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	m.t.	m.t.	1	0,03
<i>Taeniopteryx nebulosa</i>	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	m.t.	m.t.	1	0,03
<i>Baetis fuscatus</i>	m.t.	m.t.	□	m.t.	□	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	0	0,00
<i>Baetis scambus</i>	m.t.	m.t.	□	m.t.	□	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	0	0,00
<i>Siphonurus aestivalis</i>	m.t.	m.t.	□	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	0	0,00
Identified individuals	13	46	245	43	103	38	14	23	12	591	310	165	1420	3023	77,10
<i>Siphonurus</i> sp	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0,03
Perlidae	1	0	0	0	1	0	0	0	3	0	0	0	0	5	0,13
<i>Isoperla</i> sp.	0	0	0	6	5	0	0	0	0	0	0	0	0	11	0,28
<i>Nemoura</i> sp	1	0	0	0	6	0	0	5	6	8	16	1	0	43	1,10
<i>Capnias</i> sp	2	63	69	21	0	127	18	300	223	0	0	9	0	832	21,22
<i>Leuctra</i> sp.	0	0	0	0	0	1	0	0	2	0	3	0	0	6	0,15
Total number of individuals	17	109	315	70	115	166	32	328	246	599	329	175	1420	3921	100,00
Number of missing taxa	19	16	8	12	12	14	21	16	15	13	12	14	14	14,3	

Annex B. Plecoptera and Ephemeroptera larvae in Surber samples from Vollen. Species not identified but possibly present as a component of an unidentified taxon are marked by □. Species is not present in the samples are indicated as missing taxa (m.t.).

Year	1987	1988	1989	1990	1991	1992	1993	1994	1995	1997	1998	1999	2000	2001	2002	Total	%
# sampling series per year	4	5	1	2	4	3	2	4	1	3	3	3	2	2	2	41	2,73
<i>Baetis rhodani</i>	1255	637	98	474	4415	1556	2586	728	18	1390	1249	2411	1726	1814	1699	22056	88,43
<i>Diura nanseni</i>	59	14	3	25	32	31	11	36	6	19	128	83	47	22	27	543	2,18
<i>Capnia atra</i>	1	□	□	4	51	24	2	□	m.t.	□	□	115	16	46	□	259	1,04
<i>Isoperla obscura</i>	m.t.	□	m.t.	□	1	2	45	10	□	16	5	□	14	48	68	209	0,84
<i>Ephemerella aurivillii</i>	42	6	1	2	20	43	6	5	m.t.	2	m.t.	1	1	4	15	148	0,59
<i>Taeniopteryx nebulosa</i>	28	m.t.	m.t.	25	11	18	m.t.	7	m.t.	2	1	1	10	1	17	127	0,51
<i>Isoperla grammica</i>	m.t.	□	m.t.	□	27	2	2	□	□	□	□	7	72	3	m.t.	113	0,45
<i>Protonemura meyeri</i>	1	1	m.t.	2	25	14	10	2	m.t.	m.t.	1	2	5	m.t.	2	65	0,26
<i>Amphinemura borealis</i>	□	□	m.t.	6	18	26	2	1	m.t.	1	1	m.t.	2	1	4	62	0,25
<i>Ameletus inopinatus</i>	3	1	m.t.	m.t.	26	13	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	2	m.t.	46	0,18
<i>Brachyptera risi</i>	m.t.	m.t.	1	1	14	2	10	m.t.	m.t.	2	m.t.	5	1	4	2	42	0,17
<i>Baetis subalpinus</i>	2	m.t.	m.t.	m.t.	27	2	m.t.	m.t.	m.t.	1	m.t.	5	m.t.	m.t.	m.t.	37	0,15
<i>Leuctra nigra</i>	3	8	m.t.	m.t.	m.t.	m.t.	16	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	27	0,11
<i>Amphinemura sulcipectus</i>	□	□	m.t.	1	8	1	6	m.t.	m.t.	1	m.t.	1	m.t.	3	m.t.	21	0,08
<i>Leuctra hippopus</i>	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	18	18	0,07
<i>Heptagenia joernensis</i>	m.t.	m.t.	m.t.	m.t.	1	10	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	12	0,05
<i>Leuctra fusca</i>	1	□	□	□	1	1	m.t.	m.t.	m.t.	m.t.	m.t.	5	1	m.t.	m.t.	9	0,04
<i>Capnopsis schilleri</i>	m.t.	m.t.	m.t.	1	m.t.	7	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	8	0,03
<i>Heptagenia dalecarlica</i>	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	7	m.t.	m.t.	m.t.	m.t.	1	m.t.	m.t.	8	0,03
<i>Leuctra digitata</i>	1	□	□	2	□	□	m.t.	m.t.	m.t.	m.t.	□	m.t.	□	1	2	6	0,02
<i>Siphonoperla burmeisteri</i>	m.t.	m.t.	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	3	m.t.	m.t.	m.t.	m.t.	4	0,02
<i>Baetis multicus</i>	m.t.	m.t.	m.t.	m.t.	m.t.	4	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	4	0,02
<i>Nemurella pictetii</i>	m.t.	1	m.t.	m.t.	m.t.	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	2	0,01
<i>Siphonurus aestivalis</i>	□	□	□	□	m.t.	m.t.	2	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	2	0,01
<i>Nemoura avicularis</i>	m.t.	□	□	1	□	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	□	m.t.	2	0,01
<i>Baetis fuscatus/scambus</i>	m.t.	m.t.	m.t.	m.t.	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	0,00
<i>Nemoura cinerea</i>	m.t.	□	m.t.	m.t.	□	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	□	m.t.	0	0,00
Identified individuals	1396	674	104	545	4677	1757	2699	797	24	1434	1388	2636	1897	1949	1854	23831	95,54
<i>Diura</i> sp.	17	2	0	0	0	0	0	0	0	0	2	0	44	0	0	65	0,26
<i>Amphinemura</i> sp.	3	6	0	0	2	0	0	0	0	0	0	0	0	1	0	12	0,05
<i>Isoperla</i> sp.	0	5	0	25	134	137	41	9	4	14	24	172	0	13	0	578	2,32
<i>Nemoura</i> sp.	0	2	0	0	91	0	0	0	0	0	0	0	0	3	0	96	0,38
<i>Capnia</i> sp.	15	13	4	37	53	0	0	5	0	24	8	0	0	0	110	269	1,08
<i>Leuctra digitat/fusca</i>	2	5	1	13	26	9	0	0	0	0	1	0	2	0	0	59	0,24
<i>Siphonurus</i> sp.	9	22	1	1	0	0	0	0	0	0	0	0	0	0	0	33	0,13
<i>Baetis</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0,00
Total number of individuals	1442	729	110	621	4983	1903	2740	811	28	1472	1423	2808	1943	1966	1964	24943	100,00
Number of missing taxa	13	9	18	10	9	8	14	16	23	16	17	15	13	12	16	13,9	0,06

Annex C. Plecoptera and Ephemeroptera larvae in Surber samples from Solbakken. Species not identified but possibly present as a component of an unidentified taxon are marked by □. Species not present in the samples are indicated as missing taxa (m.t.).

Year	1987	1988	1989	1990	1991	1992	1993	1994	1995	1997	1998	1999	2000	2001	2002	Total	%
Sampling series pro year	4	4	1	1	4	2	2	4	1	3	3	3	2	2	2	38	
<i>Baetis rhodani</i>	138	118	16	109	788	121	91	480	4	166	203	1120	757	830	123	5064	45.04
<i>Ephemerella aurivillii</i>	128	38	24	14	25	1	47	26	3	11	71	31	732	52	116	1319	11.73
<i>Baetis fuscatus/scambus</i>	50	393	47	m.t.	70	m.t.	89	95	4	182	124	83	m.t.	m.t.	61	1198	10.66
<i>Heptagenia dalecarlica</i>	46	15	2	2	17	9	6	63	m.t.	47	122	110	86	33	66	624	5.55
<i>Diura nanseni</i>	111	22	26	13	58	1	16	68	7	57	65	72	27	19	15	577	5.13
<i>Heptagenia joernensis</i>	68	19	32	□	44	1	31	39	14	72	16	22	m.t.	1	m.t.	359	3.19
<i>Baetis subalpinus</i>	2	8	26	m.t.	11	m.t.	3	63	1	53	65	16	11	5	52	316	2.81
<i>Baetis muticus</i>	19	15	2	4	13	8	5	83	m.t.	22	50	6	21	11	m.t.	259	2.30
<i>Amphinemura borealis</i>	□	4	1	16	74	14	1	4	m.t.	12	m.t.	m.t.	17	25	m.t.	168	1.49
<i>Ameletus inopinatus</i>	m.t.	m.t.	m.t.	m.t.	28	11	30	9	m.t.	9	1	m.t.	m.t.	3	m.t.	91	0.81
<i>Ephemerella mucronata</i>	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	□	m.t.	m.t.	1	16	18	1	m.t.	m.t.	36	0.32
<i>Leuctra fusca</i>	2	5	□	3	□	2	□	□	m.t.	4	7	9	□	m.t.	2	34	0.30
<i>Taeniopteryx nebulosa</i>	1	1	m.t.	m.t.	8	1	m.t.	m.t.	m.t.	m.t.	2	6	2	2	2	25	0.22
<i>Leuctra digitata</i>	□	□	□	□	1	□	3	□	m.t.	□	1	m.t.	□	m.t.	5	10	0.09
<i>Siphonoperla burneisterei</i>	1	2	m.t.	m.t.	m.t.	m.t.	1	m.t.	m.t.	1	m.t.	m.t.	m.t.	4	1	10	0.09
<i>Amphinemura sulcipectus</i>	m.t.	m.t.	m.t.	m.t.	7	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	2	m.t.	9	0.08
<i>Capnia atra</i>	□	□	m.t.	m.t.	2	1	m.t.	□	m.t.	m.t.	m.t.	2	m.t.	4	□	9	0.08
<i>Leuctra nigra</i>	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	7	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	7	0.06
<i>Protonemura meyeri</i>	m.t.	m.t.	m.t.	m.t.	5	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	6	0.05
<i>Leuctra hippopus</i>	4	m.t.	m.t.	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	5	0.04
<i>Nemoura</i> sp.	m.t.	m.t.	m.t.	m.t.	4	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	5	0.04
<i>Isoperla grammatica</i>	m.t.	□	m.t.	m.t.	1	1	2	m.t.	m.t.	m.t.	□	m.t.	□	m.t.	□	4	0.04
<i>Isoperla obscura</i>	m.t.	m.t.	m.t.	m.t.	1	m.t.	1	m.t.	m.t.	1	m.t.	m.t.	m.t.	m.t.	1	4	0.04
<i>Heptagenia sulphurea</i>	□	m.t.	m.t.	□	□	□	m.t.	m.t.	m.t.	□	m.t.	3	m.t.	m.t.	m.t.	3	0.03
<i>Baetis lapponicus</i>	□	1	m.t.	m.t.	m.t.	m.t.	□	m.t.	□	m.t.	m.t.	1	m.t.	1	m.t.	3	0.03
<i>Siphonurus</i> sp.	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	0.01
<i>Nemurella pictetii</i>	m.t.	m.t.	m.t.	m.t.	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	0.01
<i>Leptophlebiidae</i>	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	m.t.	1	0.01
Identified individuals	570	642	176	161	1158	172	336	930	33	638	743	1499	1654	992	444	10148	90.26
<i>Isoperla</i> sp.	0	1	0	0	122	11	0	0	0	0	2	0	5	0	3	144	1.28
<i>Perlodidae</i> (=nanseni?)	0	9	0	0	0	0	2	0	0	25	0	0	84	0	0	120	1.07
<i>Amphinemura</i> sp.	4	12	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0.14
<i>Baetis</i> sp.	2	0	0	0	0	0	1	0	2	0	0	0	0	0	0	5	0.04
<i>Heptagenia</i> sp.	13	0	0	3	8	2	0	0	0	15	0	0	0	0	0	41	0.36
<i>Ephemerella</i> sp.	0	0	0	0	0	0	2	0	0	0	0	0	525	0	0	527	4.69
<i>Leuctra fusca/digitata</i>	17	3	6	74	78	2	2	10	0	24	12	0	14	0	0	242	2.15
Total number of individuals	606	667	182	238	1366	187	343	940	35	702	757	1499	2282	992	447	11243	100
Number of missing taxa	11	11	17	18	7	13	7	15	21	12	14	14	16	14	15	13.7	



Age and growth of Siberian sculpin (*Cottus poecilopus*) and young brown trout (*Salmo trutta*) in a subalpine Norwegian river

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Key words: Subalpine river, *Salmo trutta*, *Cottus poecilopus*, age, growth, density

Abstract

Age, growth and density of Siberian sculpin (*Cottus poecilopus*) and young brown trout (*Salmo trutta*) within two sections of River Atna; above Lake Atnsjøen [Section 1 at altitudes between 739 and 715 m] and below Lake Atnsjøen [Section 2 at altitudes between 430 and 370 m] was studied during a 6-year period (1986–91). The water temperature was considerably lower in Section 1 than in Section 2, as the number of days with a water temperature above 10 °C ($T_{D \geq 10^\circ\text{C}}$) from spring to August 1 ranged between 2–26 and 26–52 days, respectively. Juvenile brown trout (age 0+) attained a significantly smaller body size in Section 1 than in Section 2; mean length \pm SD was 35 ± 8 mm (ranged 27–46) and 43 ± 7 mm (range 38–46), respectively. In Section 2, there was a highly positive correlation between the body length of 0+ brown trout and mean water temperature in June ($p < 0.005$), and also to some extent in Section 1 ($p = 0.11$). Individuals of age 1+ did not exhibit any such difference, while fish in age group 2+ were larger in Section 1 than in Section 2. By using the number of days with a water temperature between the range 5–10 °C ($T_{D \geq 5-10^\circ\text{C}}$) as test variables, we found a highly positive correlation between the August 1 body length of 0+ brown trout and $T_{D \geq 9^\circ\text{C}}$ from spring to August 1 in Section 2 ($p < 0.05$), as opposed to $T_{D \geq 7^\circ\text{C}}$ for trout in Section 1 ($p = 0.11$). Young Siberian sculpin (age 0+ and 1+) also exhibited slower growth in Section 1 than in Section 2, but this was not the case among older specimens. In the year with the lowest temperature measured (1987), no 0+ Siberian sculpin were caught in any of the two sections, indicating that low temperature affects their survival. Both species exhibited large spatial and temporal variation in density. Thus, data on abundance and growth sampled on one occasion at one site can not be regarded as representative for these two fish populations.

Introduction

In northern Europe, brown trout (*Salmo trutta*) is the dominant fish species in inland rivers and streams. The abundance of young trout is rarely in an equilibrium as their changes in numbers may be caused by negative density dependent factors in favourable streams, and by positive density-dependent and density-independent factors in unfavourable streams (Elliott 1984, 1985, 1987). Among environmental variables, water flow is often likely to have the greatest

influence on the abundance of young salmonids in streams (Milner et al., 1981; Solomon, 1985). In a cold Norwegian river young brown trout experienced the highest mortality in years with low water temperature at emergence and high discharge during the alevin stage (Jensen & Johnsen, 1999). There may also be different adaptation strategies of Atlantic salmon populations to extreme climates in cold Norwegian rivers (Jensen & Johnsen, 1986).

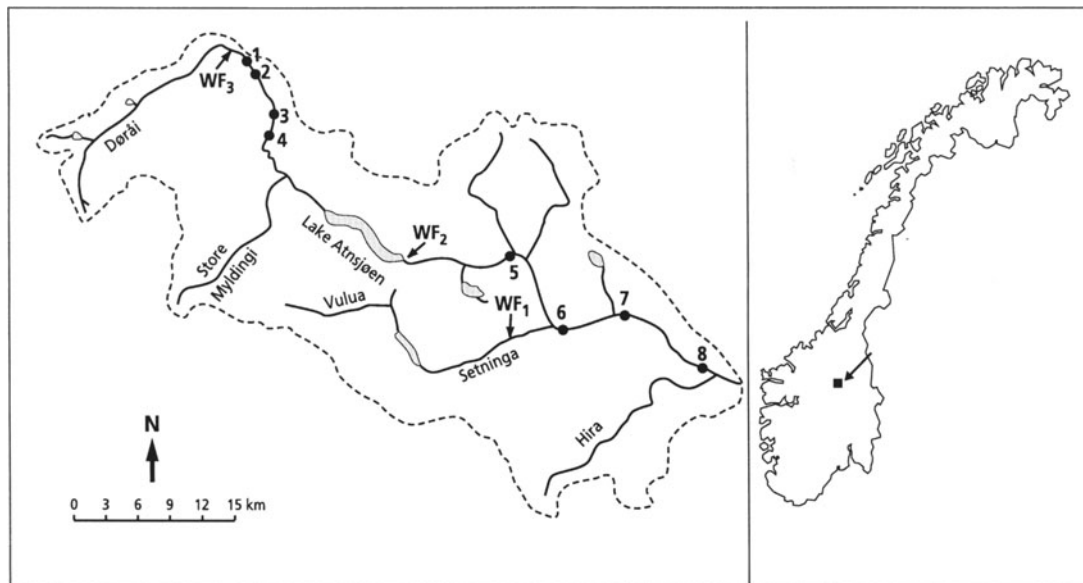


Figure 1. Geographic location and outline of Atna catchment area with different sampling stations in River Atna (1–8). The locations of the waterfalls at Solligarden (WF₁), Atnbrufossen (WF₂) and Liafossen (WF₃) are indicated. Fossum is located close to Station 7.

Spatial variations in growth and production among juvenile salmonids has been observed within different streams and rivers. In the upper part of the large River Alta in northern Norway, young Atlantic salmon (*Salmo salar*) grew faster than conspecifics in two sections down stream, which was related to the impact of an upstream lake (Heggberget et al., 1986). The lake outlet water is a direct and indirect source of nourishment for salmonids in downstream areas and cause delayed cooling of the water in the autumn (cf. Haraldstad et al., 1987). Growth differences among young Atlantic salmon have also been observed within smaller rivers (Lund & Heggberget, 1985). The growth of Atlantic salmon and brown trout fry in Scottish rivers has been shown to correlate with temperature conditions and population densities of Atlantic salmon fry (Egglishaw & Shackley, 1977). An inverse relationship between growth of Atlantic salmon fry and cohort densities has also been observed (Egglishaw & Shackley, 1980). In two streams in New Brunswick, Canada, Atlantic salmon and brown trout fry had the highest growth rate in areas of high water temperature and low population density (Randall, 1982). In a small nutrient-rich and relatively warm river in southwestern Norway, spatial variation in growth and density of young Atlantic salmon and brown trout was related to a gradient in nutrient loading (Bergheim & Hesthagen, 1990).

In the present study we investigated the age and growth of Siberian sculpin (*Cottus poecilopus*) and young brown trout within different reaches of a sub-alpine Norwegian river during a 6-year period. We paid special attention to relationship between water temperature regimes and spatial and temporal variation in fish growth.

Study area

The study areas are in the unregulated River Atna in southeastern Norway (61° 51' N, 10° 13' E), which is 97 km long (Fig. 1). The river originates in mountainous areas at an altitude of between 1400–1500 m, and confluence with River Glomma at an altitude of about 338 m. Lake Atnsjøen, at an altitude of 701 m, is the only lake in the main stem.

Brown trout and Siberian sculpin are the dominant species of fish in River Atna. Siberian sculpin, which spawn in the spring, are found throughout the main river to Liafossen waterfall about 14 km upstream of Lake Atnsjøen (cf. Fig. 1, Hesthagen & Sandlund, 2004). Resident brown trout occur throughout the river. In addition, the brown trout in Lake Atnsjøen spawn in the river, on stony reaches between 10–14 km from the lake, up to Liafossen waterfall, in the outlet river (to Atnbrufossen waterfall), and in tributary streams. River Atna downstream of Lake

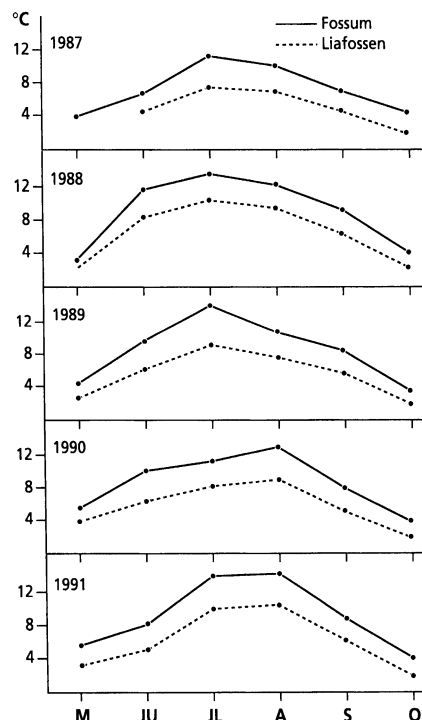


Figure 2. Mean monthly water temperatures from May to October in Section 1 (Liafossen, close to Station 1 shown in Fig. 1) and Section 2 (Fossum Bru, close to station 7 in Fig. 1) in River Atna, 1987–1991.

Atnsjøen is important spawning ground for brown trout in River Glomma (Linløkken, 1993). Brown trout in Atna catchment mainly spawn in October. Grayling (*Thymallus thymallus*) and European minnow (*Phoxinus phoxinus*) may occasionally be found in River Atna, but only downstream of Lake Atnsjøen.

The catchment area of River Atna is 1323 km², and consists mainly of slowly weathering rocks such as granite and gneiss. The upper part of the catchment area is treeless mountainous areas, while birch and pine cover areas at lower altitudes. The annual mean discharge of River Atna during the study period between 1986–91 was about 10 m³ s⁻¹ (Tvede, 2004). Predominant surface water velocities at normal summer and early autumn flow typically range between 0.4 and 1.5 m s⁻¹ (Hesthagen et al., 2004). Riffle areas with stones of 5–45 cm in diameter dominate the river bed below Lake Atnsjøen. For 10 km above the lake, River Atna flows quite slowly, and the river bed consists mainly of fine material. From 10 km above the lake up to Liafossen waterfall at 14 km upstream, the substratum is similar to the that in the outlet river, but the river channel is more unstable. The river bars and banks often migrate, and the rocky substratum

is disrupted, with subsequent high sediment transport (Bogen, 1997).

River Atna is low in nutrients and nearly neutral to slightly acid with mean annual values of calcium and pH that generally range between 0.4–1.9 mg l⁻¹ and 6.0–6.5, respectively (Blakar et al., 1997). The water temperature is lower above than below Lake Atnsjøen (Tvede, 2004) (Fig. 2). At Liafossen in Section 1, the number of days with a water temperature above reach 10 °C range between 2–26 days, as opposed to 26–52 days at Fossum Bru in Section 2 below Lake Atnsjøen. Mean water temperature in June in the two areas ranged between 4.6–8.2 and 6.6–11.6 °C, respectively (1987–1991).

Material and methods

Sampling stations were located in two sections of the river; between 10–14 km upstream and 9–17 km downstream of Lake Atnsjøen, at altitudes between 735–700 and 430–370 m, respectively (Fig. 1). A portable electrofishing apparatus (1600 V, DC) was used to sample fish between August 7 and September 4 during a 6-year-period (1986–91). Electrofishing was carried out along the river bank, generally at four stations in Section 1 (Station 1–4) and 3–4 stations in Section 2 (Station 5–8), and always in an upstream direction. The surveyed area at each station usually covered a width and length of 7–9 and 15–25 m, respectively. The water depth typically ranged between 5 and 30 cm at these stations. Densities were estimated by the successive removal method, based on total catches from all stations in each section that year (cf. Bohlin, 1981; Bohlin et al., 1989). The total length of each fish was measured after each run, and they were generally released after the final fishing run. For brown trout separate estimations were made for 0+ and ≥1+ age groups in both sections, which was determined by the length-frequency distribution. For Siberian sculpin, only ≥1+ fish were included in these estimates because juveniles (0+) were less than 25 mm in August/September, which gives very low catch efficiency. During 1986–90, each station was electrofished twice, as opposed to three times in 1991. The probability of capture (*p*) ranged from 0.46 to 0.70 for both species. In 1986, and from 1989 to 1991, the sites were fenced with nets of 5 mm bar mesh before sampling. In 1986, we placed a net pouch in the downstream stop-net to catch fish potentially displaced during electrofishing, but no fish was caught.

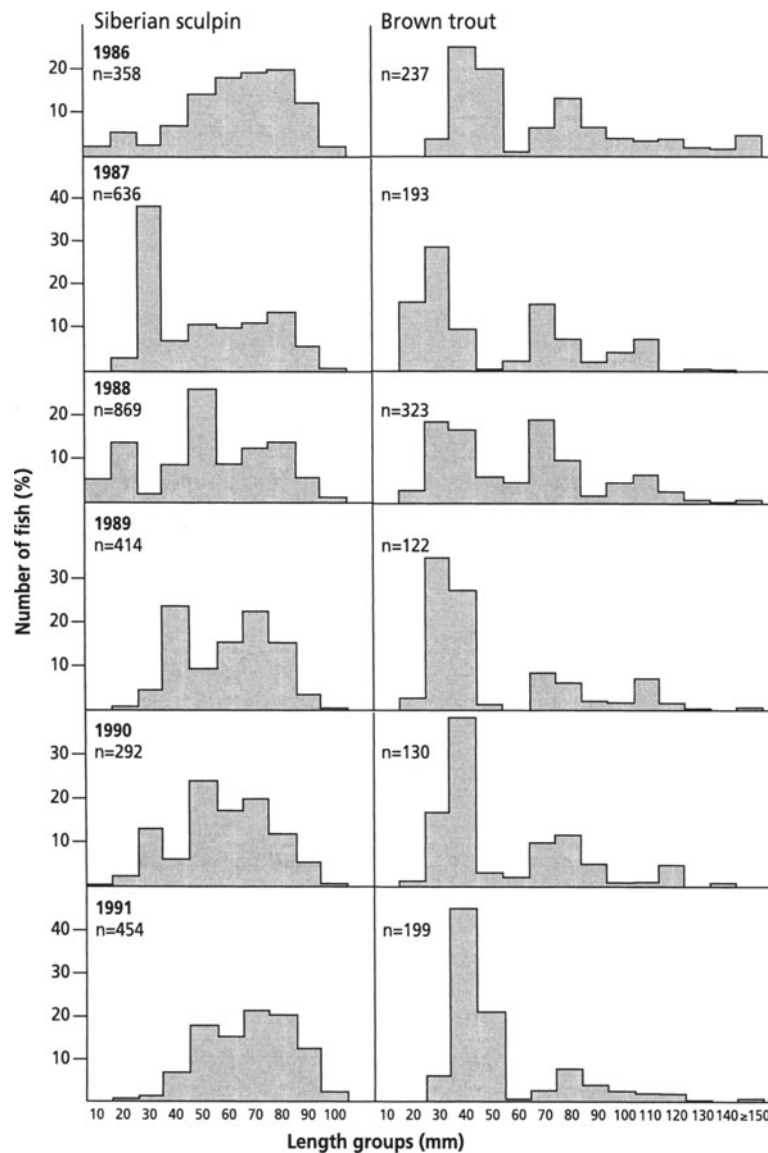


Figure 3. Length frequency distribution of Siberian sculpin and brown trout caught by means of electrofishing in River Atna, 1986–1991.

Some individuals from each station were stored for later analysis of age and growth. Siberian sculpin were aged from otoliths, and brown trout from both otoliths and scales. As the sampling took place at different times each year, the size of 0+ brown trout was recalculated to a common sampling date (August 1). This was carried out by assuming a constant daily specific growth rate from the time of emergence (determined to June 15, based on spawning time in mid October and the prevailing water temperature in the river (Jensen et al., 1991; Arne Jensen, pers. comm.).

The size attained by juvenile brown trout (age 0+) in each section each year was related to the water temperature, which was recorded continually in both Section 1 (Liafossen close to Station 1, cf. Fig. 1) and Section 2 (Fossum Bru close to Station 7, cf. Fig. 1). Water temperatures were not available from 1986.

Table 1. Mean body length (mm \pm standard deviation, L \pm SD) for different age groups of brown trout and Siberian sculpin caught in River Atna, 1986–1988, separated into samples above and below Lake Atnsjøen, Section 1 and Section 2, respectively. n = number of fish.

Age	Brown trout				Siberian sculpin			
	Section 1		Section 2		Section 1		Section 2	
	L \pm SD	N	L \pm SD	N	L \pm SD	n	L \pm SD	n
0	35 \pm 8	118	43 \pm 7	187	20 \pm 5	15	23 \pm 5	36
1	76 \pm 13	28	78 \pm 8	181	34 \pm 4	240	47 \pm 8	50
2	124 \pm 15	14	111 \pm 10	90	55 \pm 7	113	54 \pm 10	37
3	153 \pm 22	6	143 \pm 14	12	68 \pm 9	67	71 \pm 12	56
4	195 \pm 4	4	169 \pm 0.0	1	78 \pm 8	89	80 \pm 11	66
5	222 \pm 45	2			84 \pm 10	84	82 \pm 12	41
6	229 \pm 0.0	1			86 \pm 6	43	86 \pm 12	15
7			278 \pm 0.0	1	88 \pm 6	7	90 \pm 10	7
8					86 \pm 8	5	85 \pm 8	4
9							96 \pm 7	4
10					81 \pm 0.0	1		

Results

Size and growth

The body length of Siberian sculpin and brown trout ranged between 16–102 mm and 21–278 mm, respectively. Few individuals were larger than about 90 mm among Siberian sculpins and 110 mm among brown trout (Fig. 3). Most specimens of Siberian sculpin were of age 0+ to 6+, as opposed to age 0+ to 2+ for brown trout (Table 1). There was some annual variations in the age distribution of young brown trout within the river, indicating temporal variability in recruitment. In particular, there were few $\geq 1+$ fish in Section 1 in 1987–1989 (Fig. 4).

Juvenile brown trout (age 0+) above Lake Atnsjøen was significantly smaller than conspecifics below the lake, with mean values \pm SD of 35 \pm 8 and 43 \pm 7 mm, respectively (t -test, $p < 0.0001$, Table 1). No corresponding difference was found for 1+ brown trout ($p > 0.05$), while age 2+ fish had a larger body size in Section 1 (124 \pm 15 mm) than in Section 2 (111 \pm 10 mm) ($p < 0.0001$). Siberian sculpin also exhibited a slower growth rate above than below Lake Atnsjøen, but significant differences were only found for individuals of age 0+ (20 \pm 5 vs. 23 \pm 5 mm, $p < 0.05$) and age 1+ (34 \pm 4 vs. 47 \pm 8 mm, $p < 0.0001$).

Observed mean lengths of 0+ brown trout in Section 1 and Section 2 ranged between 27–46 and 38–46 mm, respectively, during the study period (Table 2).

Table 2. Mean body length (mm \pm standard deviation, L \pm SD) for juvenile (age 0+) brown trout in River Atna separated into Section 1 (above Lake Atnsjøen) and Section 2 (below Lake Atnsjøen), 1986–1991. n = number of fish.

Year	Section 1		Section 2	
	L \pm SD	n	L \pm SD	n
1986	42 \pm 6	13	48 \pm 5	52
1987	27 \pm 4	38	38 \pm 4	59
1988	36 \pm 6	50	43 \pm 7	78
1989	33 \pm 4	33	41 \pm 4	48
1990	33 \pm 4	15	42 \pm 5	69
1991	46 \pm 7	27	46 \pm 6	117

Specimens from reaches below Lake Atnsjøen were significantly larger than conspecifics above the lake ($p < 0.05$), except in 1991 ($p > 0.05$). The lengths of 0+ brown trout in Section 1 and 2, based on adjusted values to a common sampling date, were related by means of a multiple regression to selected independent variables: (i) mean density of 0+, (ii) mean density of $\geq 1+$ conspecifics, (iii) mean density of $\geq 1+$ Siberian sculpin, (iv) number of days (T_D) with a water temperature between the range 5–10 °C ($T_{D \geq 5-10^\circ C}$) from spring to August 1, and (v) mean monthly water temperature in June and July. In Section 2, there was a highly positive correlation between the August 1 body length of 0+ brown trout and mean water temperature in June ($F_{1,2} = 311.94$, $R^2 = 0.99$, $p < 0.005$,

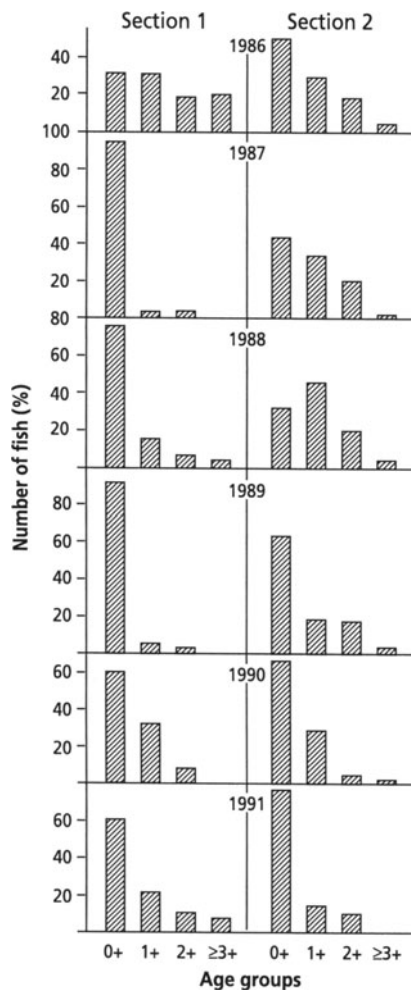


Figure 4. The age distribution of brown trout caught in Section 1 and 2 in River Atna, 1986–1991. Fish caught in 1989–1991 were separated into different age groups according to age-length data in previous years.

Fig. 5A). This correlation also verged on being significant for trout in Section 1 ($F_{1,3} = 12.76$, $R^2 = 0.80$, $p = 0.07$). By using the number of days with a water temperature that ranged between 5 and 10 °C ($T_{D \geq 5-10^\circ\text{C}}$) from spring to August 1 as independent variables, we found that the size of brown trout fry at August 1 was best correlated with $T_{D \geq 9^\circ\text{C}}$ in Section 2 ($F_{1,3}=38.31$, $R^2=0.93$, $p<0.05$) (Fig. 5B). The best corresponding relationship between growth and water temperature in Section 1 was found for $T_{D \geq 7^\circ\text{C}}$, which verged on being significant ($F_{1,3} = 7.58$, $R^2 = 0.69$, $p = 0.11$).

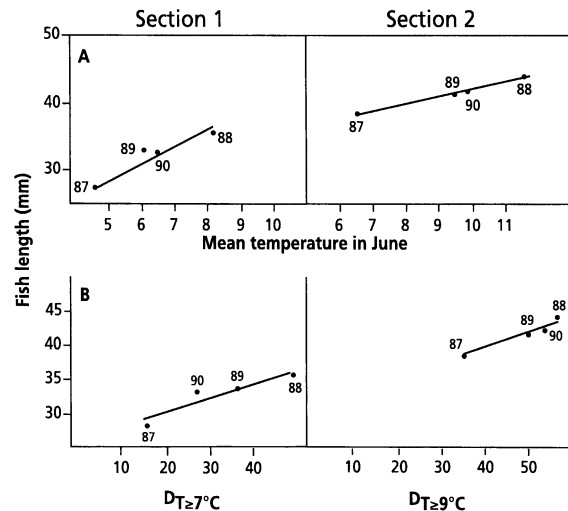


Figure 5. A: Relationship between mean length (ML) of 0+ brown trout at August 1 in Section 1 and Section 2 in River Atna, and mean water temperature in June (T_j). The equations for the two variables, with standard error were; Section 1: $ML = 2.23 \pm 0.62 * T_j + 18.30 \pm 4.02$, Section 2: $ML = 1.01 \pm 0.06 * T_j + 31.32 \pm 0.55$. B: Relationship between ML of 0+ brown trout at August 1 and number of days with a water temperature $\geq 7^\circ\text{C}$ from spring to August 1 in Section 1 was; $ML = 0.21 \pm 0.08 * T_{D \geq 7^\circ\text{C}} + 25.39 \pm 2.72$ and that of $\geq 9^\circ\text{C}$ during the same period in Section 2; $ML = 0.21 \pm 0.03 * T_{D \geq 9^\circ\text{C}} + 31.08 \pm 1.60$. Numbers given at different points indicate year of investigation (1987–1990). The size of 0+ brown trout in 1991 diverged highly from that expected from the temperature regime that year, and was excluded from the analysis.

Density

The highest densities of brown trout were recorded at stations below (Section 2) Lake Atnsjøen (Mann–Whitney U -test, $p < 0.0005$). Mean densities of 0+ brown trout were about 2.8–13.8 times higher in Section 2 than in Section 1 in 1986–87 and 1990–91, while differences were small in 1988–89 (Table 3). Similarly, the densities of $\geq 1+$ fish were 2.4–13.3 times higher in Section 2 than in Section 1 in 1986 and 1989–91, while in 1987–88 densities of these age groups were 2.3–3.7 times higher in Section 1. Siberian sculpin was most abundant above Lake Atnsjøen (Mann–Whitney U -test, $p < 0.0005$). Mean densities of $\geq 1+$ Siberian sculpin in Section 1 were 2.1–4.7 times higher than in Section 2 during 1989–91, while the differences in 1986–88 were small.

Discussion

The temperature regime in River Atna is far beneath what is considered to provide optimal growth condi-

Table 3. The density $100 \text{ m}^{-2} \pm 95\%$ confidence limits of brown trout (BT) and Siberian sculpin (SS) of 0+ and $\geq 1+$ age groups in River Atna from 1986 to 1991, separated in Section 1 (above Lake Atnsjøen) and Section 2 (below Lake Atnsjøen).

Species	Age groups	Section	1986	1987	1988	1989	1990	1991
BT	0+	1	0.6 ± 0.2	3.9 ± 1.9	5.5 ± 0.8	11.1 ± 5.6	3.7 ± 1.5	6.0 ± 2.1
	0+	2	8.3 ± 2.3	10.9 ± 2.4	5.4 ± 1.1	14.8 ± 2.9	31.4 ± 7.1	29.8 ± 4.3
	$\geq 1+$	1	1.1 ± 0.6	12.9 ± 13.5	14.7 ± 3.4	0.8 ± 0.4	2.5 ± 1.2	3.5 ± 0.6
	$\geq 1+$	2	8.2 ± 1.5	3.5 ± 1.6	6.3 ± 1.0	10.6 ± 4.1	10.9 ± 3.1	8.3 ± 1.1
SS	$\geq 1+$	1	12.5 ± 5.1	61.5 ± 27.0	44.5 ± 10.2	103.4 ± 16.2	56.3 ± 6.3	67.9 ± 3.1
	$\geq 1+$	2	17.7 ± 9.7	65.1 ± 21.5	43.0 ± 6.3	22.0 ± 3.4	21.1 ± 5.3	32.6 ± 10.1

tions for brown trout (Elliott, 1995). This is especially the case in the upper reaches of the river where the temperature may reach 10°C only for a short period of time each year, i.e. between 2–26 days during our study period of 6 years (cf. Fig. 2). Juvenile brown trout (0+) and Siberian sculpin (0+ and 1+) from this area grew slower than conspecifics from areas further down stream, e.g. below Lake Atnsjøen. Thus, our data suggest that the prevailing water temperature affect the growth of young brown trout within River Atna differently. However, we cannot reject a genetic component for this spatial variability in growth, and other abiotic and biotic factors may also be of importance for the observed growth patterns. The study area in the upper part of River Atna is located at about 300 m higher altitude than the downstream study area. Thus, the upper area has a longer period of snow-melt, and in addition this river stretch receive influx of groundwater (Tvede, 2004). The water temperatures in the river rise faster in down-stream areas, where Lake Atnsjøen also has a positive impact.

Lengths of brown trout fry in the autumn were positively correlated with mean water temperature in June. Their lengths were also positively correlated with the number of days in June and July with water temperatures above 7°C in upper reaches (Section 1) and above 9°C in lower reaches (Section 2). This difference in growth pattern may reflect different adaptation strategies to extreme climates within the two sections, as as found for Atlantic salmon in some cold Norwegian rivers (Jensen & Johnsen, 1986). In 1987, the mean water temperature in the upstream section was only 4.6°C in June, as opposed to between 5.1 – 8.2°C for other years. The water temperature in June is probably of special importance for brown trout in River Atna because they are expected to emerge

from the gravel in the middle of that month. Warm years probably have a positive effect on their growth, both directly through higher metabolism and indirectly through higher food production.

In addition to slow growth among juvenile brown trout in River Atna in 1987, this cohort seems to be especially low in numbers in upstream sections. The reason for this may be that low water temperature is the predominant mortality factor for brown trout during emergence (Jensen & Johnsen, 1999). It has earlier been shown that low temperatures at the swim-up stage affect swimming performance in brown trout (Heggenes & Traaen, 1988). Water discharges during emergence may also affect their survival, although critical threshold values are difficult to establish (Jensen & Johnsen, 1999). The discharge in River Atna during the emergence of brown trout varied highly during the study period, but was not extraordinary during spring 1987 (Tvede, 2004). However, during high discharge in River Atna there is typically a strong increase in sediment transport and the stream bed becomes highly unstable (Bogen, 1997). It is likely that these conditions have a detrimental effect on the survival of young fish in the river (cf. Berg & Northcote, 1985).

There is no inverse relationship between growth and density in young brown trout in River Atna. This differs from investigations on other salmonid species in running water (Egglishaw & Shackley, 1977; Randall, 1982; Bergheim & Hesthagen, 1990). However, at low densities, populations of brown trout is probably controlled by abiotic factors rather than by density dependent factors. It is well known that physical disturbances maintain populations at low densities (Huston, 1979). In two contrasting English Lake District streams, perturbation by spates and droughts

caused brown trout rarely to reach equilibrium densities (Elliott 1985, 1987). Rather, in the favourable stream sustaining high brown trout densities, population density changes were caused by negative density dependent factors, whereas in the unfavourable stream with low density positive density-dependent factors were important.

There was no difference in the size of 1+ brown trout between Sections 1 and 2, while two-year-old fish were larger in Section 1. This may be related to size-selective mortality through higher mortality among young fish during winter because these individuals have lower energy reserves. The fact that the density of 0+ brown trout was generally lower in upper reaches of River Atna may also have a positive effect on their growth rate. The age structure of young brown trout in both upper and lower reaches of the river indicates that most specimens leave the river and migrate into Lake Atnsjøen and River Glomma, respectively, during their first year of life. The disappearance of any variation in size among 1+ brown trout within the river may also be connected to size-selective time of this migration between these two areas.

The low temperatures in June 1987 also appeared to have a strong negative impact on Siberian sculpin as no juveniles were caught during electrofishing in the autumn this year. The poor 1987 cohort was also verified from the sample in the following year as few 1+ fish were caught. Among the possible mechanisms through which water temperature may direct or indirect influence the abundance of juvenile sculpin are food availability, spawning initiation and duration and high post-hatching mortality. For two darters species, *Etheostoma simoterum* and *E. rufilineatum*, it was suggested that cooler water in spring one year delayed spawning initiation and perhaps altered spawning duration (Greenberg, 1988). In River Atna, the water flow was at a normal level in spring 1987, so it is unlikely that high discharges had any negative effect on the recruitment of Siberian sculpin. Thus, a weak year-class of Siberian sculpin this year may rather be connected to low water temperatures.

Acknowledgements

Financial support was received from the Norwegian Council for Scientific and Industrial Research and the Directorate for Nature Management. Thanks are due to Ånund Kvambekk at Norges vassdrags – og energi-

direktorat (NVE) for providing water temperature data for River Atna and to Odd Terje Sandlund for valuable comments to this paper.

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Niche overlap between young brown trout (*Salmo trutta*) and Siberian sculpin (*Cottus poecilopus*) in a subalpine Norwegian river

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Key words: Subalpine river, *Salmo trutta*, *Cottus poecilopus*, density, diet, habitat use, interactions

Abstract

The density, diet and habitat use of brown trout (*Salmo trutta*) and Siberian sculpin (*Cottus poecilopus*) were studied in the subalpine River Atna in southeastern Norway in the autumn during a six year period (1986–1991). There was an inverse relationship between the density of brown trout and Siberian sculpin. Diet overlap, as indicated by the Schoener index, was high between the two species, ranging between 0.48 and 0.86. Chironomid larvae and other aquatic insects were the most common food items for both species. Brown trout also consumed substantive amounts of surface insects. Siberian sculpin typically occupied sites with finer substrates and greater water depths than brown trout, even though there was considerable overlap in habitat use between the two species. Because the two species shared similar habitats, we suggest that the potential for species interactions exists, particularly at sites where density of sculpin is high.

Introduction

Competition from non-game fishes in streams is believed to have a negative impact on salmonid populations. However, the evidence for this is weak (Brown & Moyle, 1981). Freshwater sculpins (family Cottidae) are often abundant in streams suitable for salmonids (Andreasson, 1969; Le Cren 1969; Mann, 1971; Petrosky & Waters, 1975; Mills & Mann, 1983; Mann et al., 1989). Spatial variation in the density of Atlantic salmon (*Salmo salar*) and brown trout (*Salmo trutta*) in several Swedish rivers indicate that these two salmonids are negatively affected by the presence of bullheads (*Cottus gobio*) (Karlstrøm, 1977). However, Glova (1987) suggested that *Cottus* sp. do not compete significantly with salmonids in streams.

Several authors have discussed trophic interactions between sculpins and salmonids. While sculpins apparently feed only on bottom fauna (Bailey, 1952; Straškraba et al., 1966; Brocksen et al., 1968; Pet-

rosky & Waters, 1975), salmonids obtain most of their food from drift (Ringler, 1979; Bachman, 1984; McNicol et al., 1985). Andreasson (1971) found that bullhead and young brown trout consumed similar food in spring in a Swedish stream, but their diets differed in summer and autumn, which he suggested illustrated diminishing competition through interactive segregation. However, in another Swedish stream, there was little interaction between these two species (Olsson & Näslund, 1983). In a sub-Arctic river in northern Norway, Atlantic salmon parr and Siberian sculpin (*Cottus poecilopus*) had high diet overlap from spring to late fall, and it was suggested that interspecific competition for limited food resources explains the low production of Atlantic salmon in the river (Gabler & Amundsen, 1999). However, in another river in northern Norway, introduced bullheads seem to affect the habitat use of Atlantic salmon to only a limited extent (Jørgensen & Amundsen, 1997; Jørgensen et al., 1999). Furthermore, the diets of bullhead and Atlantic

salmon parr in this system indicated selective segregation (Gabler et al., 2001). Petrosky & Waters (1975) found that slimy sculpin (*C. cognatus*) and brook trout (*Salvelinus fontinalis*) exploited similar food resources in a Minnesota (U.S.A.) stream, but interspecific competition was not apparent. Even though sculpins and salmonids have different foraging behaviour, sculpins may compete with drift-feeding salmonids by cropping benthic food organisms and thereby reducing the amount of drift (Brocksen et al., 1968; Glova, 1987). The density of the two species obviously will influence the level of competition in cases where niche overlap does occur.

Competitive interactions between stream-dwelling fishes might also involve resources such as space or positions, as shown between the two morphologically similar salmonid species, brown trout and brook trout (Fausch & White 1981). However, there may also be competition for space between morphologically dissimilar species, such as riffle sculpin (*C. gulosus*) and speckled dace (*Rhinichthys osculus*) (Baltz et al., 1982). Similarly, experimental studies suggest that brown trout may be displaced from preferred streambed substrata by Siberian sculpin (Hesthagen & Heggenes 2003).

In this study, we investigated the population density, food habits and habitat use of brown trout and Siberian sculpin in River Atna, a subalpine Norwegian river, to assess the possible interactions between the two species, based on the extent of niche and habitat overlap, and negative association between species abundances.

Study area

The unregulated River Atna (61° 51' N, 10° 13' E) originates in the Rondane National Park in southeastern Norway at an altitude of nearly 1500 m (Fig. 1). The river is 97 km long and has one lake (Lake Atnsjøen) on its main stem at an altitude of 701 m. River Atna drains into the River Glomma at 338 m. The catchment area of River Atna is 1323 km², and consists mainly of slowly weathering rocks such as granite and gneiss. The uppermost part of the watershed is treeless mountains, and birch and pine cover the area at altitudes lower than about 1000 m. The annual mean discharge rate in River Atna between 1930 and 1960 was 10.3 m³ s⁻¹ (Tvede, 2004). The corresponding discharge during the study period, i.e. from 1986 to 1991, was 10.0 m³ s⁻¹. The maximum

value of 94.9 m³ s⁻¹ was reached during spring snow melt in 1990. Predominant surface water velocities at normal summer flow typically range between 0.4 and 1.5 m³ s⁻¹. Riffle areas with stones of 5–45 cm in diameter predominates the river 10–14 km upstream of Lake Atnsjøen, as well as throughout the river below the lake. The river bed 0–10 km above the lake consists mainly of sand. The river bed is more unstable above than below the lake (Bogen, 1997).

The temperature of the river system varies considerably with altitude and season (Tvede, 2004). Upstream of Lake Atnsjøen the river is cold owing to influx of groundwater and a long snowmelt period, and temperatures seldom reach 10 °C in July–August. Downstream of Lake Atnsjøen, the temperature may reach 12–13 °C. The river is slightly acid and has low levels of dissolved solids, with mean annual values for pH and calcium concentration between 6.0–6.5 and 0.4–1.9 mg l⁻¹, respectively (Blakar et al., 1997).

Brown trout and Siberian sculpin are the predominant species of fish in River Atna. The distribution of Siberian sculpin in the main river is restricted by Lifossen waterfall about 14 upstream of Lake Atnsjøen (cf. Fig. 1, Hesthagen & Sandlund, 2004). Brown trout in Lake Atnsjøen spawn mainly in the inlet river 10–14 km upstream from the lake, in the lake outlet, and in some smaller lake tributaries. Downstream of Lake Atnsjøen, brown trout from River Glomma migrate into River Atna, to spawn (Linløkken, 1993). A very few grayling (*Thymallus thymallus*) and European minnows (*Phoxinus phoxinus*) occur downstream of Lake Atnsjøen (Hesthagen & Sandlund, 2004).

Methods

Fish populations were sampled at seven or eight locations with a portable electrofishing apparatus (1600 V) in an upstream direction in August or early September, 1986–1991 (Fig. 1). The total sampling area was between 710–1515 m² each year. The sampling stations were located in reaches 10–14 km upstream of Lake Atnsjøen (715–739 m) and 9–17 km downstream of Lake Atnsjøen (370–430 m). Electrofishing was carried out along the river bank, and individual sampling stations usually covered widths of 7–9 m and lengths of 15–25 m.

Densities were estimated by the successive removal method (Zippin, 1958; Bohlin et al., 1989). During the period 1986–1990, each station was electrofished twice, while sampling effort was increased

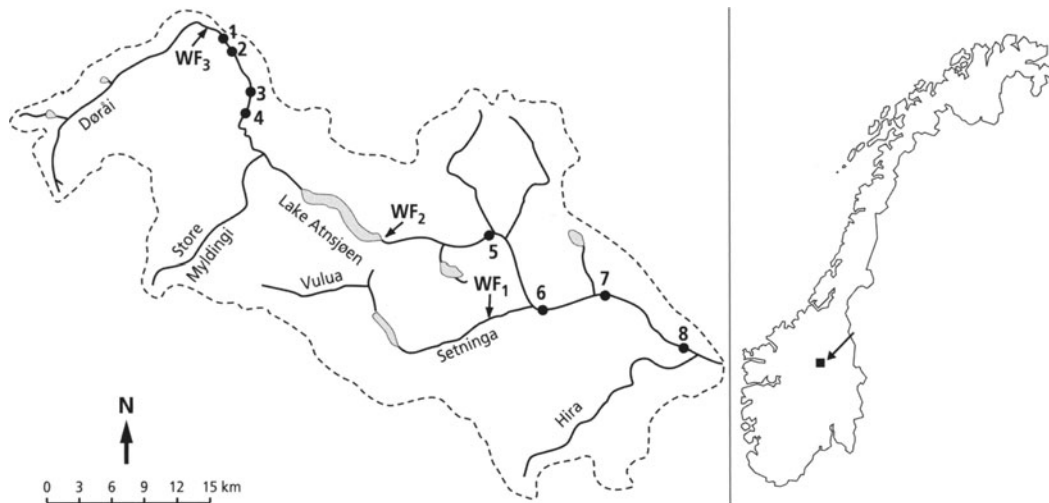


Figure 1. The watershed of River Atna showing the location of Lake Atnsjøen, and the fish sampling stations in the river. The locations of the three main waterfalls within the watershed are shown: WF₁ [Solligarden], WF₂ [Atnbrua] and WF₃ [Liafossen].

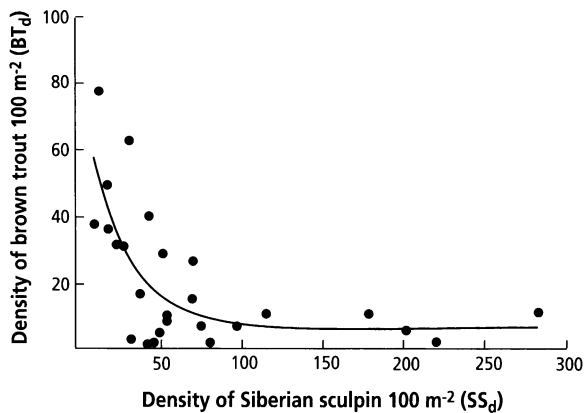


Figure 2. Relationship between densities (number of fish per 100 m²), of brown trout (BT_d), and Siberian sculpin (SS_d) from the sampling stations in River Atna, 1986–1991, expressed by the equation: $BT_d = 6.04 + 77.41 \exp -0.0398 SS_d$. Stations with densities lower than 30 fish 100 m⁻² of either species were excluded from the regression (see text).

to three times in 1991 (Hesthagen et al., 2004). For brown trout, we made separate estimates for 0+ and ≥1+ age groups, based on length–frequency distributions. The total length of fish in these two age groups typically ranged between 30–60 and 70–120 mm, respectively. We did not estimate densities of age 0+ Siberian sculpin as they had reached a length of less than 25 mm in August/September, and consequently had very low catch efficiency. Thus, population estimates for Siberian sculpin included fish of age ≥1+, typically individuals larger than 40 mm.

We analysed the stomach contents of brown trout and Siberian sculpin from sampling areas above and below Lake Atnsjøen throughout the six-year period (1986 to 1991). The stomach content of individual fish was stored in 70% alcohol. For brown trout, we distinguished between small and large fish (30–60 and 70–120 mm; see above). For Siberian sculpin, small and large fish constituted individuals of about 30–45 mm (age 1+ and 2+) and 50–100 mm (age ≥3+), respectively. For each stomach, the number of animals in different taxonomic groups was counted, and the size of a sample of food items was measured, ranging between 25 to 100% depending on the number of specimens in each stomach. For various food items we either measured head width or body length (excluding appendages). The regression equations given by Hindar et al. (1988) were used to calculate the dry weights of other zoobenthos, chironomid larvae and surface-living insects. The dry weight proportion of each food category in each stomach was then used to calculate the relative percentage composition (W%). Fragments of plants made up only a smaller fraction of the stomach contents and were excluded from the analysis. We made separate measurements of food items eaten by small and large specimens of both Siberian sculpin and brown trout. Primary data were used to calculate dry weight (W , mg) from the head widths (H , mm) and body lengths (L , mm) for both Plecoptera [$\log W = 3.63 \log H - 0.43$, $R^2 = 0.87$, $p < 0.00001$, $n = 100$], Ephemeroptera [$\log W = 3.20 \log H - 0.53$, $R^2 = 0.91$, $p < 0.00001$, $n = 119$] and Trichoptera [$\log W =$

Table 1. Diet overlap (Schoener's index) between different size classes (small vs. large) of brown trout (BT) and Siberian sculpin (SS) in River Atna, 1986–1991.

Test groups	1986	1987	1988	1989	1990	1991
Small BT vs. small SS	0.55	0.72	0.69	0.86	0.50	0.52
Large BT vs. larger SS	0.78	0.71	0.76	0.61	0.48	0.63
Small BT vs. large SS	0.61	0.69	0.72	0.81	0.51	0.54
Large BT vs. small SS	0.72	0.70	0.75	0.65	0.56	0.69

$1.83 \log L - 1.36$, $R^2 = 0.60$, $p < 0.00001$, $n = 21$]. Trichopteran body lengths (L_T) were estimated from the regression between L and H , using specimens similar in size to those found in River Atna (H was usually between 0.4 and 1.5 mm) [$\log L_T = 1.08 \log H + 0.97$, $R^2 = 0.85$, $p < 0.00001$].

We used the percent similarity index D for calculating diet overlap between small and large specimens of brown trout and Siberian sculpin (Schoener, 1968):

$$D = 1 - 0.5 \sum_{i=1}^n (p_i - q_i),$$

where p_i and q_i are the proportions by weight of food item i in species 1 and 2, respectively, and n is the number of food categories. D varies between 0 and 1.0, representing no to complete food overlap, respectively. The degree of overlap in diet between two species is considered significant when the index is greater than 0.60 (Wallace, 1981).

We tested differences in habitat use by brown trout and Siberian sculpins with respect to water depth, streambed stones, water velocities and distance from the river bank. We separated the fish into small and large size groups, similar to that used in the diet analysis. Water depths were classified according to where each fish was caught as <10 cm, 10–20 cm, 20–30 cm, etc., and that of the substratum into four categories: <5 cm, 5–15 cm, 15–45 cm and >45 cm in the diameter of dominant stone size. Fish caught at different distances from the river bank were grouped as being at <0.1 m, 0.1–0.4 m, 0.5–1.0 m, and then for each metre.

Results

Density relationship

For the total data set, the density of brown trout of age $\geq 0+$ decreased significantly with increasing densities of Siberian sculpin of age $\geq 1+$ (linear regression, $p < 0.05$, $R^2 = 0.10$, 48 sampling incidences).

Assuming the biotic interactions are small or non-existing at low populations densities, i.e. below carrying capacity (Power et al., 1988), we omitted the data from low-density stations. Low densities may be controlled by abiotic factors, such as physical disturbances (Huston, 1979). Based on sampling incidences with a minimum of 30 fish 100 m⁻² of either species (26 samples), densities of brown trout decreased significantly with increasing Siberian sculpin densities (non-linear regression, $R^2 = 0.73$, $p < 0.01$) (Fig. 2). In some cases, densities of Siberian sculpin reached values between 100 and 280 fish 100 m⁻².

Diet

Small brown trout ($n = 209$) had consumed mainly surface insects, chironomid larvae, Ephemeroptera nymphs and various other aquatic insect larvae (Fig. 3). The abundance of surface insects in the diet varied considerably, being great in years when chironomid larvae were scarce. The diet of small Siberian sculpin ($n = 210$) resembled that of small brown trout, though surface insects were nearly absent from the sculpin diet. On average, chironomid larvae made up 37 W% (range 5–70) and 42 W% (range 27–79), of the diet of small brown trout and Siberian sculpin, respectively. Large brown trout ($n = 207$) rarely consumed chironomid larvae, but otherwise their diet was similar to large Siberian sculpin ($n = 278$). Among large fish, the most common food item of both species was Trichoptera larvae, with an average value of 33 W% (range 20–51) for brown trout and 35 W% (range 11–46) for Siberian sculpin. However, in five out of six years, large Siberian sculpin consumed fewer surface insects, and more chironomid larvae than large brown trout. Piscivory was recorded only once in both Siberian sculpin and brown trout.

Diet overlap between brown trout and sculpin as expressed by Schoener's index was relatively high irrespective of the size-groups of the two fish species;

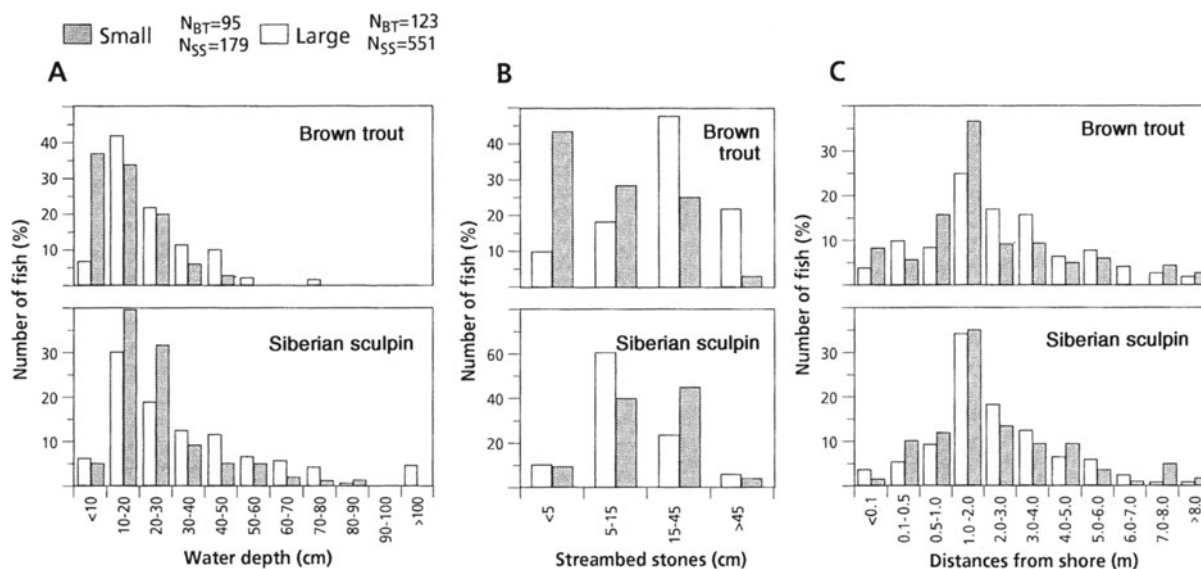


Figure 3. Relative percent frequency of occurrence of small and large brown trout and Siberian sculpin in River Atna in relation to water depth (A), streambed stones (B) and distance from the river bank (C). N_{BT} and N_{SS} represent numbers of brown trout and Siberian sculpin, respectively.

0.50–0.86 for small individuals, 0.48–0.78 for large individuals and 0.51–0.81 for small vs. large individuals of either species (Table 1). Significant overlap ($D > 0.6$) was recorded in 17 out of 24 comparisons. The diet overlap differed among years. All overlap indices were significant in three (1987, 1988 and 1989) out of six years. In one (1990) of the six years, all overlap indices were not significant.

Habitat use

There were generally significant differences in habitat use between brown trout and Siberian sculpin in River Atna (Table 2). Brown trout of both size groups were often caught at depths of less than 20 cm, whereas sculpin usually occurred at depths of 10–30 cm (Fig. 4A). Small sculpin were associated with a coarser substrate than small brown trout (Fig. 4B). Small brown trout were often associated with relatively fine gravel (stones <5 cm, 42%), whereas small sculpin occurred in approximately equal numbers in areas with 5–15 cm (41%) and 15–45 cm stones (44%). Large Siberian sculpin were often (61%) associated with stones of 5–15 cm, whereas a large proportion (49%) of large brown trout were associated with stones of 15–45 cm.

Brown trout generally occupied areas closer to the river bank than Siberian sculpin (Fig. 4C), but the differences were not statistically significant (Chi-square

test, $p > 0.05$). Individuals of both species were often caught at distances of between 1.0 and 2.0 m from the river bank.

Discussion

The density of brown trout in River Atna was lower at stations that supported high densities of Siberian sculpin, which in some cases reached 100–280 fish aged $\geq 1+$ 100 m⁻². The inverse correlation in density may indicate a significant level of interaction between the two species. This may be related to factors such as the availability of shelter, which Greenberg (1988) related to substrate composition in different species of fish in streams. He suggested that this may be connected to energetic costs because coarse substrates create refuges from fast current and predation, and substrate use is also related to differences in foraging behaviour, and to the abundance and availability of food resources. Although we found some habitat segregation between brown trout and Siberian sculpin in River Atna, there was considerable habitat overlap. For instance, about 50% of small brown trout were associated with the same type of streambed material as most Siberian sculpin. Fausch & White (1981) demonstrated that brown trout excluded brook trout from resting positions beneath cover in a stream, which was regarded as a critical and scarce resource. Resting

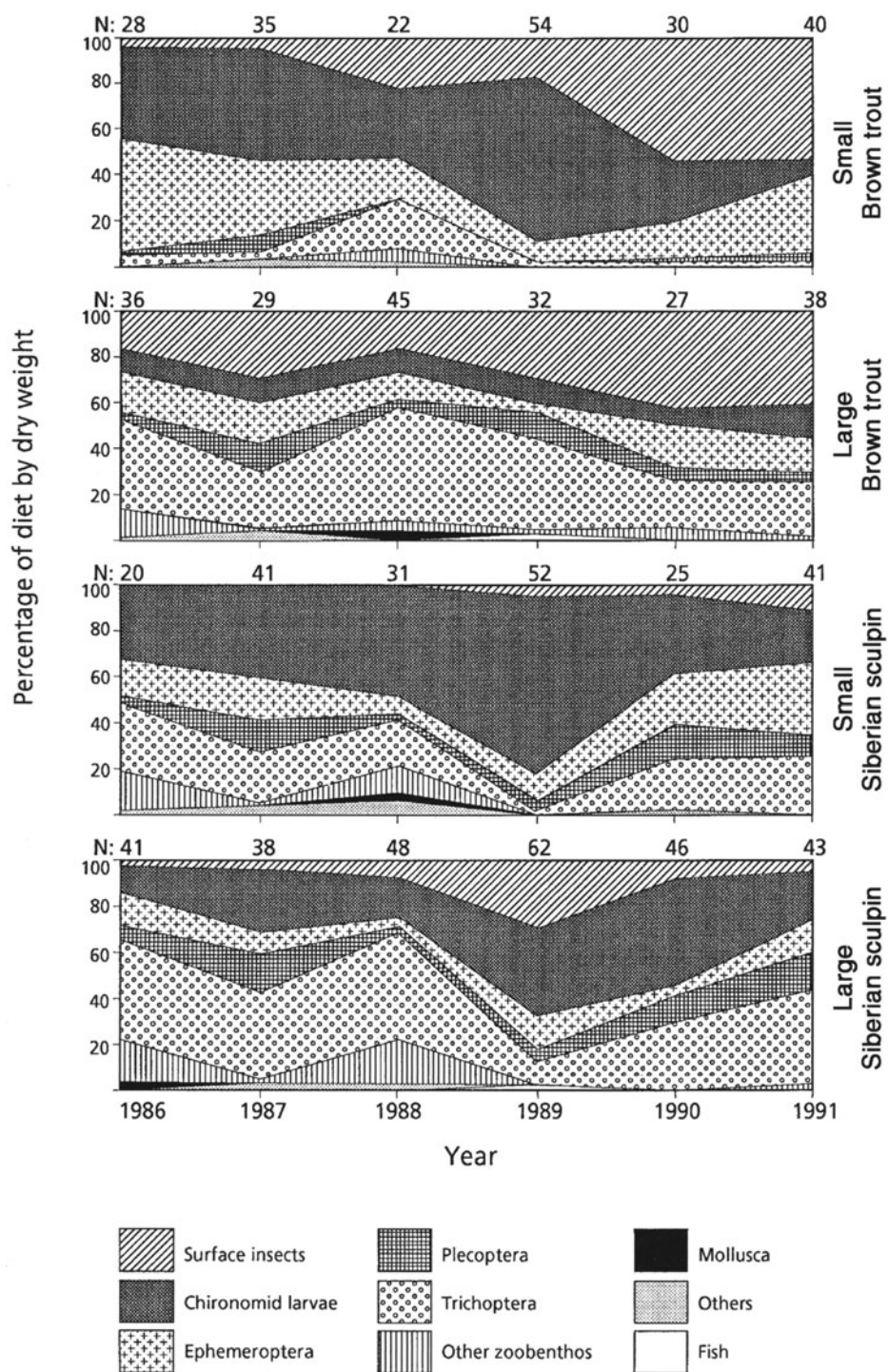


Figure 4. Percent composition by dry weight ($W_{\%}$) of food items in stomachs of small and large brown trout (BT) and Siberian sculpin in River Atna, 1986–1991. N = number of stomachs examined.

Table 2. Chi-square test for interspecific differences in habitat use in small and large specimens of brown trout (BT) and Siberian sculpin (SS) in River Atna. Subscripts of the chi-square values are degrees of freedom. ns = not significantly different ($p > 0.05$)

Variable	Small BT vs. small SS		Large BT vs. Small SS		Small BT vs. Large SS		Large BT vs. Large SS	
Water depth	50.9 ₈	$p < 0.00001$	11.0 ₃	ns	100.9 ₁₀	$p < 0.00001$	26.8 ₁₀	$p < 0.005$
Streambed gravel	40.6 ₃	$p < 0.00001$	25.9 ₃	$p < 0.00001$	66.8 ₃	$p < 0.00001$	84.1 ₃	$p < 0.00001$
Distance from river bank	12.7 ₁₀	ns	15.8 ₁₀	ns	39.1 ₁₀	$p < 0.001$	8.7 ₁₀	ns

positions also seem to be important for the abundance of sculpins in streams. Bailey (1952) observed that mottled sculpin (*C. bairdi punctulatus*) were most abundant in riffle areas that had most hiding places under rubble and boulders where they spent most of their time. He found that mottled sculpin were scarce in areas with slow currents and deposits of fine sediment, i.e. a scarcity of hiding places. Experimental studies in stream channels containing three sizes of substratum and stocked at four densities of small and large brown trout and Siberian sculpin native to River Atna, also indicated interspecific interactions, including competition for cover (Hesthagen & Heggenes, 2003). In sympatry, large Siberian sculpin preyed upon small brown trout (age 0+) and restricted trout to areas with substrate types differing from that used in allopatry. Large Siberian sculpin also affected the habitat use of large brown trout. Because the two species shared similar habitats in this experimental study, we suggest that there is a potential for species interactions in River Atna, particularly at sites with high density of Siberian sculpin.

Analysis of stomach contents indicated that Siberian sculpin and brown trout in River Atna exploited common food resources in early autumn. Important food items for both species were chironomid larvae and other aquatic insects. However, whereas brown trout to some extent consumed surface insects, these were almost absent from the diet of Siberian sculpin. Large brown trout rarely ate chironomid larvae, which was common food for both small and large Siberian sculpin. The Schoener index of diet overlap between brown trout and Siberian sculpin was relatively high, with 17 out of 24 comparisons giving an overlap index larger than 0.6. Similar results regarding diet overlap was found between Atlantic salmon parr and Siberian sculpin in a sub-Arctic river in northern Norway, ranging between 0.54–0.82 from May to October (Gabler & Amundsen, 1999). It is, however, interesting to note that in our material the degree of

diet overlap varies from year to year. We found that the diet overlap was significant ($D > 0.6$; Wallace, 1981) among all groups in three out of six years. On the other hand, in one year, none of the overlap indices were significant (i.e. $D < 0.6$). This indicates the importance of time series in assessing the interactions between fish species.

The high degree of diet overlap between salmonids and sculpins is somewhat surprising, considering their differences in feeding mode, with *Cottus* spp. as typical bottom-feeders (Straškraba et al., 1966; Petrosky & Waters, 1975). Sculpins are poor swimmers, with a poor ability to catch prey in the water column (Crisp, 1963; Western 1969). They remain on the bottom, both during rest and feeding (Roussel & Bardonnet, 1996). Brown trout, on the other hand, are generalists, taking prey both off the substratum, drifting in the water column, and on the surface (Kelly-Quinn & Bracken, 1990). The relative importance of these feeding strategies varies, as the fish may change their feeding position (Chaston, 1968; Bachman, 1984). There are obviously seasonal variations in availability and preference of food items in different species of fish. Brown trout feed more on surface insects during summer, irrespective of whether Siberian sculpin is present (Frankiewicz et al., 1993; Koksvik, 1998). Siberian sculpin do not switch to surface insects at all (Koksvik, 1998). In a laboratory experiment with *C. perplexus* and brown trout, the former species grazed so heavily on the bottom fauna that the abundance of drifting individuals was reduced, hence affecting the food base for brown trout (Brocksen et al., 1968). Field studies have shown that two *Cottus* species (*C. bairdi* and *C. girardi*) may reduce invertebrate densities (Flecker, 1984). Thus, it appears reasonable that high densities of Siberian sculpin in River Atna may negatively impact the density of brown trout.

Brown trout and Siberian sculpin may be affected differently by environmental conditions due to differences in morphology, physiology and life history.

Siberian sculpin remain under stones or on the substratum, and feed by picking aquatic insects off the stones (Bailey, 1952). It may therefore be less affected by unstable hydraulic conditions than brown trout, which spend more time in the water column feeding on aquatic drift (Bachman, 1984). These differences in use of cover and mode of feeding may indicate that Siberian sculpin tolerate a wider range of water velocities than do brown trout. Other factors, such as temperature, may mediate competitive interactions for preferred microhabitat between dissimilar species through oxygen haemoglobin affinity. Baltz et al. (1982) found that riffle sculpin (*Cottus gulosus*) displaced speckled dace (*Rhinichthys osculus*) from their sites at low temperatures, whereas this did not happen at higher temperatures.

Similar causal relationships might also exist between brown trout and Siberian sculpin densities in River Atna. The temperature was lower in the river above Lake Atnsjøen than below the lake, and Siberian sculpin densities were much higher above the lake than at stations further downstream, while the opposite was true for brown trout (Hesthagen et al., 2004). There was also large annual variation in both growth rate and density in both brown trout and Siberian sculpin. The present study also demonstrates such annual variation with respect to the diet of the two species. Thus, our results indicate that River Atna represents a relatively unfavourable river system where fish production to a large extent is controlled by density-independent factors (cf. Elliott, 1987).

Acknowledgements

Financial support was received from the Royal Norwegian Council for Scientific and Industrial Research and the Directorate for Nature Management. Thanks are due to Arnfinn Langeland for allowing us to reanalyse his data on body size and dry weight relationships for various zoobenthos groups, and to Odd Terje Sandlund and Ray White for valuable comments on the manuscript.

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LAKE ATNSJØEN



Some physical and chemical characteristics of Lake Atnsjøen

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Key words: subalpine lake, ultraoligotrophy, time series

Abstract

The physical and chemical characteristics of the dimictic, ultraoligotrophic, and subalpine Lake Atnsjøen are described based on data from the period 1985–2001. The temperature stratification of the lake is weakly developed, with the thermocline at about 10 m depth. The surface temperature during summer is usually lower than 14–15 °C. The Secchi disk transparency is normally higher than 8–10 m in summer and autumn, but can be as low as 4.3 m during spring. The pH is about 6.0, and the specific conductivity about 1.0 mS m⁻¹. The dominating cation and anion are Ca (≈0.8 mg l⁻¹ or 42 μeq l⁻¹), and SO₄ (≈1.5 mg l⁻¹ or 33 μeq l⁻¹), respectively. The concentration of bicarbonate (HCO₃, μeq l⁻¹) is sometimes lower, sometimes higher than that of SO₄.

Introduction

Hydrographical studies in Norwegian mountain lakes are few, and for short time periods only. Long time monitoring is more common in lowland lakes, often in connection with monitoring of eutrophication processes (Kjellberg, 1999). The shallow, subalpine Lake Øvre Heimdalsvatn was studied quite thoroughly during the IBP-period from 1969 to 1973 (Kloster, 1978). There are also some data from the same period from the nearby glacier fed, subalpine Lake Gjende and the clearwater alpine Lake Bessvatn (Elgmork & Eie, 1989). Some data from the same area are also given in Blakar & Jacobsen (1979).

The present paper documents the variation in some hydrographical parameters in Lake Atnsjøen over a 16 years period, from 1985 to 2001.

Lake Atnsjøen and its catchment area

Lake Atnsjøen is an oligotrophic, dimictic fjord lake situated 701 m a.s.l., with a lake surface area of 4.8 km². The watershed is 457 km², of which 85 % is situated above 1000 m a.s.l. which corresponds quite well with the treeline in the area. The lake is 80 m

deep, has a mean depths of 35.4 m and a volume of 169•10⁶ m³ (Holtan et al., 1982, Østrem et al., 1984) (Fig. 1).

The littoral zone is steep and in the upper 1–2 m the substratum is dominated by stones and gravel. The water level in the lake usually fluctuates about 0.5–1 m during the spring flood. From 1(2)–5 m the bottom is covered with a dense mat of quillwort (*Isoëtes* spp.). In the profundal zone the sediment is a typical, greyish oligotrophic gyttje (Wetzel, 2001).

The mean water discharge at the outlet of Lake Atnsjøen is 10.0 m³ s⁻¹ (Tvede, 2004). During winter the water discharge at the outlet is constant at about 2–3 m³ s⁻¹, and it is about ten times higher during summer (Tvede, 2004). During the snowmelt in May and the first part of June water flow may surpass 50 m³ s⁻¹, but only for short periods. A particularly high spring flood was observed in 1995, when the water flows were increasing from about 6 m³ s⁻¹ on 25 May to about 182 m³ s⁻¹ on 1 June, then dropping to about 80 m³ s⁻¹ on 5 June. There are normally no pronounced floods during autumn. The theoretical retention time is normally short, about 6 months, while it was only eleven days during the high flood in 1995.

The geology of the watershed is uniform, and consists mainly of feldspar quartzite (sparagmite) (Of-

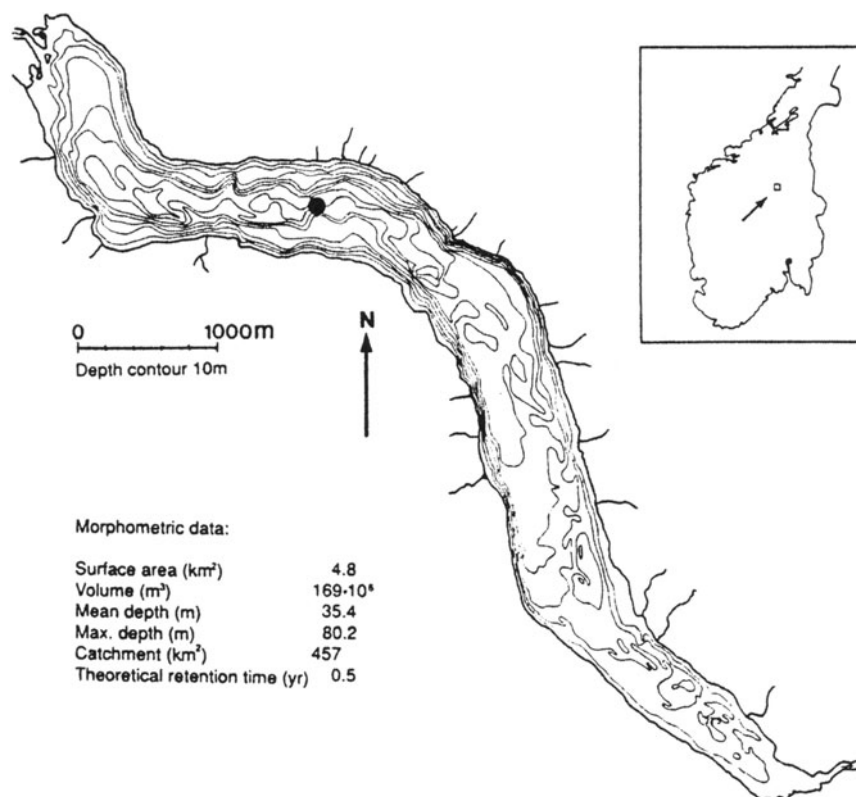


Figure 1. Morphometric map of Lake Atnsjøen, with sampling station (called B1 in text) indicated. Depth contours at 10 m intervals.

tedahl, 1950). The area has locally large deposits of Quaternary moraine and fluvial materials. There are no glaciers in the area, but permanent snowfields may remain in the highest areas during cool summers. The runoff from these does influence the water temperature during part of the summer (Tvede, 2004).

The lake is situated in an area with continental climate (Nordli & Grimenes, 2004). The mean yearly temperature during the sampling period has varied between -0.5°C in 1985 and 2.6°C in 1990, i.e. 1.2°C below and 1.9°C above the normalised value for 1961–1990 (0.7°C), respectively. The yearly precipitation has varied between 508 mm in 1989 and 673 mm in 1988, compared with the normal 555 mm. The precipitation is highest during summer and autumn, from June to October, when it falls as rain. The winter precipitation is low. The area is covered with snow from the last part of October to the beginning of May.

Lake Atnsjøen is covered with ice from the end of November to the end of May, with a mean ice-free period of 184 days (Tvede, 2004). During the study

period, the length of the ice-free period has varied between 165 days (1992/93) and 203 days (1989/90).

Material and methods

The results of Blakar et al. (1990) are mainly from the river Atna, from the catchment area north of the lake, and from the outlet of Lake Atnsjøen. Some older hydrographical data from Lake Atnsjøen itself are found in Matzow (1974), Eie (1982), Holtan et al. (1982), and Dervo (1988). These reports are, however, all in Norwegian, and a summary of these data are shown in Annex 1.

The temperature stratification has been monitored by a temperature recorder for some periods at station B1 in Lake Atnsjøen, and likewise the temperature at Atna Bridge just below the outlet have been recorded the last years. The results are presented in Tvede (2004). Parallel to this station B1 (Fig. 1) was sampled monthly from June to October, during the ice-free period, from 1985–2001.

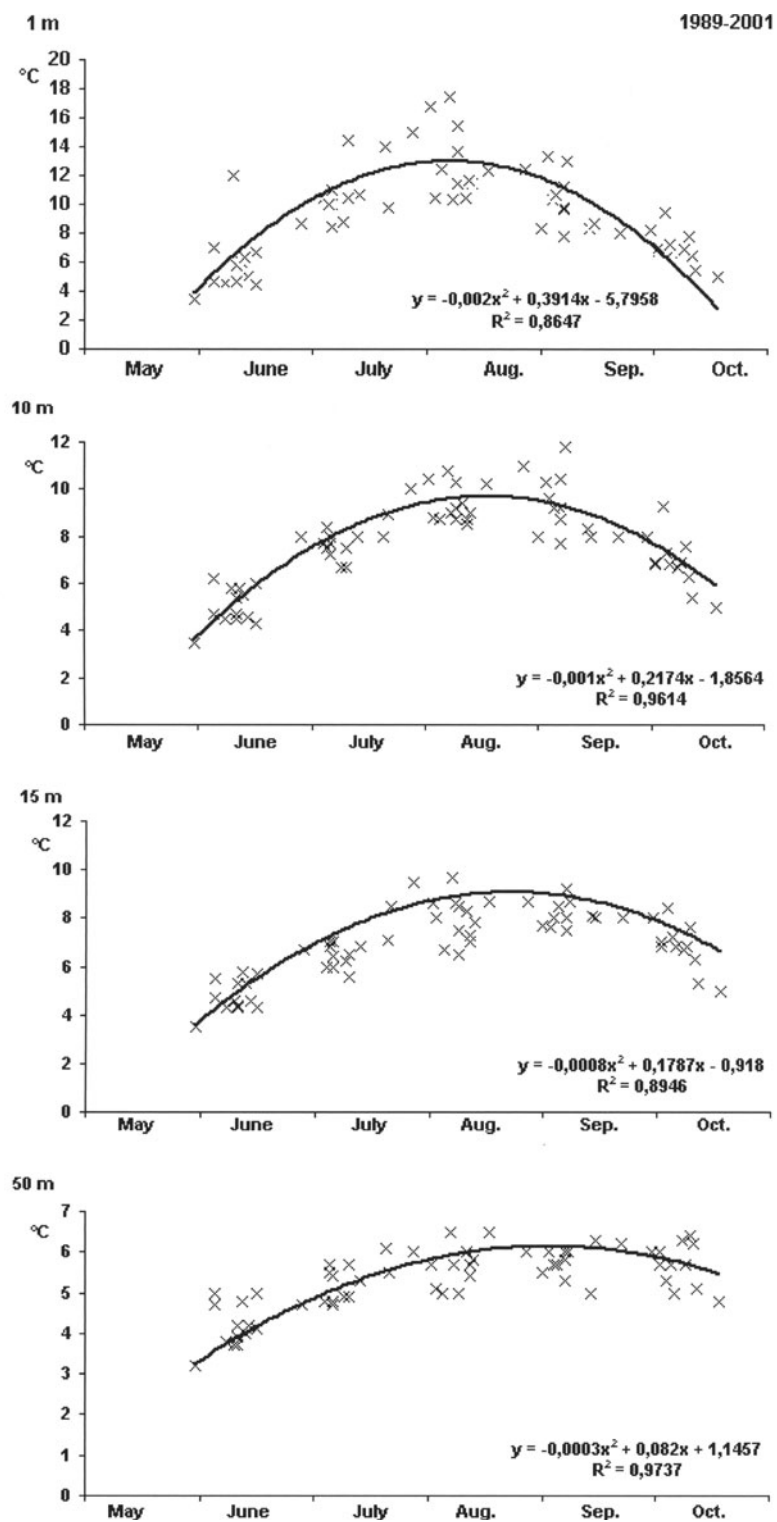


Figure 2. Water temperatures at respectively 1, 10, 15, and 50 m depth in Lake Atnsjøen during the period 1989–2001.

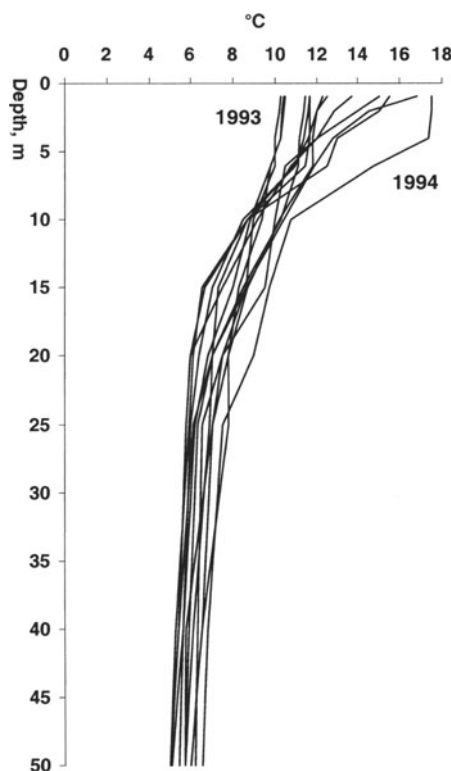


Figure 3. Temperature profiles from 1 to 50 m depth in Lake Atnsjøen at the end of July or beginning of August, at maximum surface water temperatures.

Water samples were collected by using a 2 l Ruttner water sampler with a built-in thermometer, and stored on 1 litre polyethylene bottles. The sampling program has been standardised, with samples at 1, 6, 10, 15, 20, 25 and 50 m depth. The water temperature was measured in the field at the same depths. All the water samples were analysed with respect to pH and specific conductivity (mS m^{-1}). In 1990, 1991 and 1992 also the main ions (Ca, Mg, Na, K, Fe, Mn, SO_4 , Cl, N-NO_3) were analysed according to standard methods.

The Secchi disk depth and lake water colour have been assessed at all stations. The lake colour was assessed against the white Secchi disk at half the Secchi disk depth (Strøm, 1943).

Results

Temperature

The water temperature at 1, 10, 15 and 50 m depths is given in Figure 2. In Figure 3 the vertical temper-

ature profiles at the end of July/beginning of August are given for the years 1989–2001. July–August is the time of the year with the highest epilimnetic temperature, and the most pronounced stratification. The stratification is normally not very pronounced, and the thermocline is usually situated at about 10 m depth.

The water temperature has varied substantially between years. The yearly amplitude decreases from surface to bottom. While the differences between years have been about 2°C at 50 m depth the differences at 1 m have been as much as $6\text{--}8^\circ\text{C}$. The differences at 10 and 15 m are intermediate, about 3°C . The maximum summer temperature at 10 m occurs about one month later than at 1 m.

During summer, the surface temperature normally varies between 10 and 14°C , and the hypolimnetic temperature between 3 and 6°C . The highest temperatures measured were 16.8°C and 17.5°C at 1 m, in the end of July 1991 and in the beginning of August 1994, respectively. In contrast the lowest maximum temperature measured was 10.3°C in the beginning of August 1993.

Secchi disk transparency and water colour

The Secchi disk transparency varied throughout the summer, being highest in autumn and lowest in spring and early summer (Fig. 4). It is normally higher than 8–10 m, but has varied between 4.3 m (June 1995) and 14.5 m (September 1992). The low transparency during spring is correlated with high water-flow and high input of allochthonous material. There is no, or only a very weak, correlation between transparency and the density of zooplankton.

Usually the transparency was the same at all sampling stations, but on some occasions there is a small increase in transparency towards the lake outlet. Similarly, there occasionally was an increase across the lake from station B1 to station D1, especially in autumn.

The water colour, as read against the Secchi disk at the half transparency depth varies between green and yellowish green. Yellowish green dominates during spring and early summer while green is common in autumn. Only in exceptional cases the colour was greenish yellow.

Water chemistry

Lake Atnsjøen is extremely poor in electrolytes, with a specific conductivity varying between 0.8 and 1.1 mS m^{-1} (Fig. 5, Annex 1, Annex 2). There is

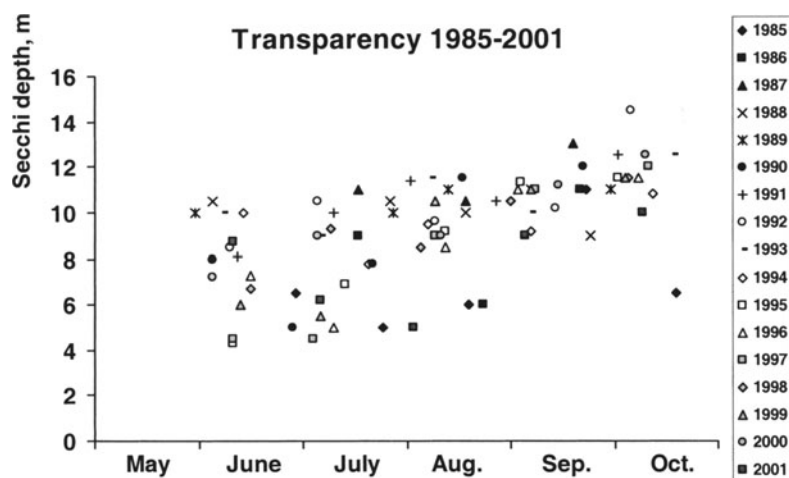


Figure 4. Secchi disk readings at station B1 in Lake Atnsjøen in the period 1985–2001.

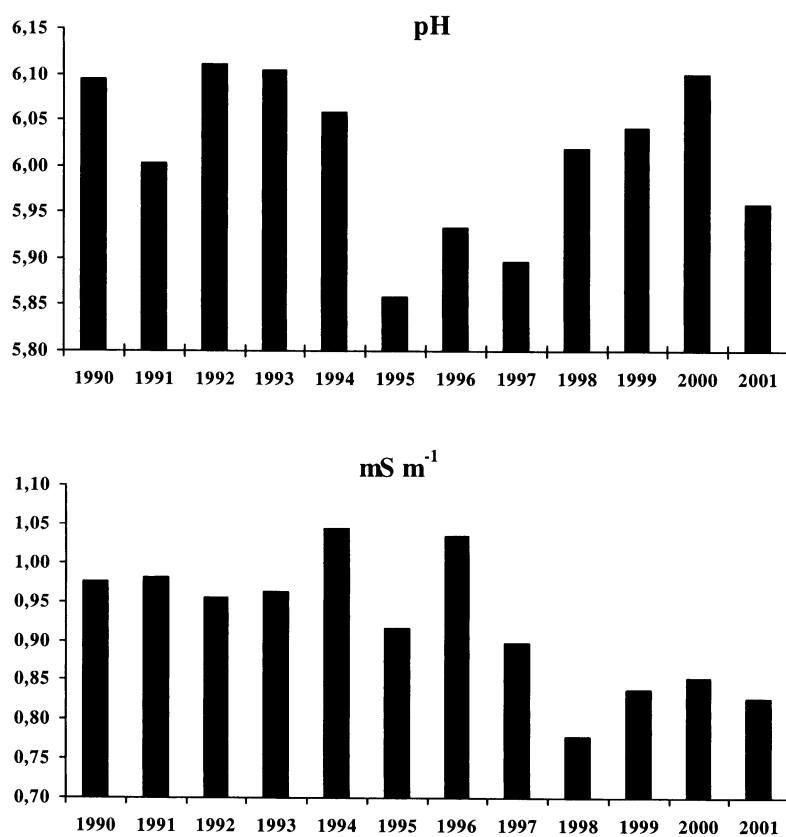


Figure 5. The mean yearly pH and specific conductivity (mS m^{-1}) based on 35 samples from 5 samplings in June to October each year during the period 1990 to 2001.

a tendency to decreasing conductivity in later years. There is only a weak chemical stratification from surface to bottom, but normally a 10–15% increase in conductivity was observed with depth.

The pH varies around 6.0, with normally a small decrease in the hypolimnion (Fig. 5, Annex 1, Annex 2). There is also a tendency that pH increases during summer. The mean pH have varied between years, with minimum values in 1995 and 1997.

Ca and SO₄ are the dominating ions, constituting about 55 and 45% of the cations and anions, respectively. The Ca content varies around 0.8 mg l⁻¹ (42 µeq l⁻¹) while the SO₄ content normally is lower than 1.5 mg l⁻¹ (33 µeq l⁻¹). The alkalinity is low, less than 50 µeq l⁻¹, indicating a very low buffering capacity. Although the chemical stratification of the lake is insignificant, there may be some minor differences between years correlated to precipitation and water flow in the main river, which influences the duration of the retention time. The concentration of Fe and Mn was always below the detection limits of the applied methods.

The oxygen conditions are typical for oligotrophic lakes with short renewal time. At the end of the summer stagnation period, the saturation are normally higher than 80% in the profundal (Annex 2), in the epilimnion always close to 100%.

Discussion

The water temperatures of Lake Atnsjøen reported here correspond well with earlier results (Tvede, 2004), with highest mean water temperature in July and beginning of August. The highest monthly mean temperature at the outlet is 12.5 °C in July (Tvede, 2004). In large fjord lakes, wind generated currents and internal seiches force deepwater up to the surface at the outlet, and the outflow is thus a mixture of surface and deep waters (Lerman, 1978). Antonsson (1992) found that the temperature at the outlet in Thingvallavatn corresponded well with the temperature at 20 m depth. In Lake Atnsjøen the corresponding depth is about 10 m (Fig. 2), but here the temperature is measured a short distance below the outlet, at Atna Bridge, which may allow some warming up of the outlet water (Tvede, 2004). The lake brings about an increase in the water temperature as the in-flowing water normally has a lower temperature than the out-flowing water. The difference is about 1.3 °C on a yearly basis. In spring and early summer the situation

may be opposite, with lower temperature at the outlet than at the inlet. This happens when high air temperatures cause a swift increase in river water after the snow melting period.

There is quite good correspondence between the water temperature in the upper part of the epilimnion and the mean air temperature at the meteorological station at Sørnesset (Tvede, 2004). There are, however, some deviations in some years due to the substantial energy storage effect of the lake, and the amount of snow left in the catchment area.

The transparency increases during summer, with reduced inlet river flow and reduced input of allochthonous material. We are, however, not able to demonstrate directly the correlation between transparency and inlet river discharge. The reason is probably that a large proportion of the allochthonous material is transported into the lake at the very beginning of an increasing flow (Bogen, 1980; 2004). The maximum phytoplankton and zooplankton densities appear to be of little importance for water transparency in Lake Atnsjøen.

The influx of water from the river will follow (due to the Coriolis force) the north-western shore towards the outlet (Lerman, 1978). During low water flow in autumn the clear water from the river will result in somewhat higher transparency along the north-western shore than in the central and north-eastern part of the lake.

The observed water colour, green or yellowish green, is typical for ultraoligotrophic and oligotrophic lakes with none or only a small influence of humic substances (Strøm, 1943). A few times the colour is greenish yellow which may indicate a more eutrophic situation with higher phytoplankton densities.

The chemical weathering in the catchment area is slow, and the water is very low in ions (Blakar et al., 1990; Blakar & Digernes, 1999). The specific conductivity rarely exceed 1.5 mS m⁻¹ and values below 1.0 mS m⁻¹ are common. In 1987 and 1998 the conductivity was even lower than 0.8 mS m⁻¹. These years were cold with high precipitation, and the dilution effect of melting snow was high during most of the summer. The observed values correspond well with values given by Kjensmo (1966) for lakes with catchment areas dominated by light sparagmite, and are typical for most of the lakes and rivers in the Rondane area (Blakar et al. 1990, Blakar & Digernes, 1999). They are also of the same magnitude as in Øvre Heimdalsvatn (Kloster, 1978), and in many other lakes

in the Jotunheimen area (Blakar & Jacobsen, 1979; Elgmork & Eie, 1989).

The buffering capacity is very low, with an alkalinity rarely exceeding $50 \mu\text{eq l}^{-1} \text{HCO}_3^-$. In periods of high flow, alkalinity as low as $3\text{--}15 \mu\text{eq l}^{-1} \text{HCO}_3^-$ is common. In some of the tributaries alkalinity may drop to zero in some periods, especially in spring. The area is thus sensitive to anthropogenic pollution, especially acid deposition. The watershed is, however, little influenced by both local and long distance anthropogenic pollution, and the lake and the watershed are excellently suited for studies of long-term natural variation and development.

The lake function as a stabilising factor in most of the chemical parameters and reduce both the short and long term fluctuation in water quality in the outlet river (Blakar & Digernes, 1999). A common trait in most of the parameters is a decrease in concentration between inlet and outlet of the lake. The stabilising effects are correlated to the retention time, even though this is quite short in Lake Atnsjøen (averaging about 6 months). The pH in the lake clearly demonstrates the stabilising effects as the yearly variation is smaller at the outlet than at the inlet (Blakar & Digernes, 1999). Normally pH vary between 5.9 and 6.3 in the lake while it can be lower than 5.5 at the inlet. In some of the higher situated lakes in the watershed the pH can be as low as 4.7–5.0, and in some of the lesser tributaries pH as low as 4.4–5.5 have been observed (Blakar & Digernes, 1999).

The pH drop in 1995, which was still detectable in 1996 and 1997, was probably caused by the especially high flood in 1995, when the proportion of groundwater runoff was small compared with the surface runoff. The relatively low pH in 2001 was correlated to high precipitation.

The content of macro-constituents corresponds well with earlier results, and with relatively small differences between years. In some years HCO_3^- was the dominating anion while SO_4^{2-} dominated in other years. This may reflect different influence of groundwater relative to surface runoff. In 1995 the concentration of Ca and Mg was similar to earlier years, while Na and K had lower concentration. Correspondingly the concentration of SO_4^{2-} and HCO_3^- was higher than in earlier years, while the Cl concentration was lower. These differences are probably related to the high flood in 1995, which flooded large wetland areas and opened large new areas for erosion (Bogen, 2004).

The content of nitrate ($\text{NO}_3\text{-N}$) in Lake Atnsjøen was quite high compared with Ø. Heimdals-

vatn (Kloster, 1978). Normally it varies around $60\text{--}70 \mu\text{g l}^{-1}$, but values between $30\text{--}90 \mu\text{g l}^{-1}$ were also common. In 1995 the mean concentration of $\text{NO}_3\text{-N}$ decreased from $150 \mu\text{g l}^{-1}$ at the inlet to $120 \mu\text{g l}^{-1}$ at the outlet (Blakar & Digernes, 1999). The higher concentration in 1995 was probably caused by the high flood with a large input of allochthonous material. The primary production in this type of lake is normally controlled by low phosphorous contents rather than by nitrogen (Wetzel, 2001).

The oxygen condition was good in all years, with only a small reduction in the deeper part of the hypolimnion towards the end of the stagnation period. Even during winter, after a long period of ice-cover, the oxygen saturation is normally higher than 60–80% in such lakes (Halvorsen & Elgmork, 1976; Elgmork & Eie, 1989; Halvorsen, unpubl.).

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Annex 1. Some physical and chemical data from station B1 in Lake Atnsjøen based on some earlier studies published in Norwegian (Matzow, 1974, Holtan et al., 1982), and unpublished data (I. Blakar, unpubl.).

	Matzow (1974)		Holtan (1982)	Blakar, unpublished			
	18.07.1974	11.10.1974	1980	11.06.1987	15.07.1987	20.08.1987	18.09.1987
	0–70 m	0–60 m	0–10 m	1–65 m	1–65 m	1–65 m	1–65 m
pH	6.1–6.5	6.2	6.14	6.09–6.15	5.98–6.07	5.89–6.19	5.88–6.15
Spec. Conduct., mS m ⁻¹			0.24–1.39	0.93–0.98	0.79–0.88	0.78–0.92	0.81–0.91
Turbidity, FTU			0.2–0.8	0.40–0.53	0.54–0.58	0.34–0.53	0.36–1.06
Colour, Pt mg L ⁻¹			12–41	8.5–9.2	7.2–9.4	6.3–9.2	6.9–9.7
Ca, mg L ⁻¹	1.19–1.39	1.04–1.06		0.78–0.86	0.69–0.72	0.61–0.74	0.59–0.68
Mg, mg L ⁻¹	0.15–0.19	0.17–0.19		0.14–0.15	0.11–0.13	0.11–0.13	0.13–0.19
Na, mg L ⁻¹	0.54–0.86	0.49–0.64		0.32–0.35	0.27–0.33	0.28–0.33	0.29–0.32
K, mg L ⁻¹	0.36–0.74	0.22–0.41		0.26–0.29	0.21–0.26	0.19–0.26	0.22–0.27
SO ₄ , mg L ⁻¹	1.92–3.22	2.64–3.46		1.72–1.81	1.40–1.58	1.16–1.57	1.27–1.55
Cl, mg L ⁻¹	0.60–1.00	0.55–0.70		0.40–0.44	0.36–0.48	0.44–0.51	0.38–0.43
Alkalinity, µeq L ⁻¹	29–53	70–107	70	60.4–62.2	51.8–56.0	41.6–47.2	41.6–46.6
NO ₃ , µg L ⁻¹			20–80	66–80	45–60	30–63	
SiO ₂ , mg L ⁻¹			2.0–2.6				
Tot-Phosphorus, P µg L ⁻¹			1.0–4.5				
O ₂ , saturation %	81–91	83–90	72–78				
Chlorophyll, µg L ⁻¹			1.1–3.5				
Secchi disk transp., m	9.5	9.5	7.7–8.0				
Water colour	Yel. green	green		Yel. green	Yel. green	Yel. green	Yel. green

Annex 2. Some physical and chemical data from station B1 in Lake Atnsjøen in 1990, 1991 and 1992. The mean values in mg l^{-1} , and $\mu\text{eq l}^{-1}$ are given in the lower part of the Annex together with the percentage ratios between cations and anions.

Date	Depth (m)	Temp. (°C)	Cond. (mS m^{-1})	pH	Ca (mg l^{-1})	Mg (mg l^{-1})	Na (mg l^{-1})	K (mg l^{-1})	SO ₄ (mg l^{-1})	Cl (mg l^{-1})	NO ₃ -N ($\mu\text{g l}^{-1}$)
4.6.90	1	7.0	1.09	6.36	0.81	0.16	0.38	0.29	1.69	0.42	66
4.6.90	6	6.5	1.10	6.01	0.84	0.16	0.38	0.29	1.71	0.43	50
4.6.90	10	6.2	1.11	6.25	0.83	0.16	0.38	0.29	1.74	0.42	68
4.6.90	15	5.5	1.09	6.20	0.83	0.16	0.39	0.30	1.70	0.43	75
4.6.90	20	5.0	1.09	6.30			0.37	0.28			
4.6.90	50	5.0	1.10	6.09	0.85	0.16	0.38	0.29	1.75	0.43	61
4.6.90	55	4.9	1.12	6.21	0.85	0.16	0.39	0.30	1.86	0.45	92
27.6.90	1	8.7	0.91	5.96	0.61	0.12	0.31	0.25	1.50	0.40	55
27.6.90	6	8.2	0.89	5.91	0.62	0.12	0.29	0.23	1.37	0.37	58
27.6.90	10	8.0	0.90	5.72	0.62	0.12	0.29	0.24	1.45	0.38	53
27.6.90	15	6.7	0.96	5.98	0.68	0.13	0.32	0.25	1.50	0.40	68
27.6.90	20	6.5	0.99	6.04	0.73	0.14	0.34	0.27	1.57	0.40	71
27.6.90	50	4.7	1.10	6.09	0.85	0.16	0.38	0.29	1.71	0.41	71
27.6.90	55										
20.7.90	1	9.8	0.91	6.00	0.67	0.13	0.33	0.25	1.42	0.37	46
20.7.90	6	9.1	0.90	5.91	0.66	0.13	0.32	0.24	1.45	0.35	47
20.7.90	10	8.9	0.89	5.99	0.66	0.13	0.32	0.24	1.43	0.37	47
20.7.90	15	8.5	0.89	6.00	0.67	0.13	0.32	0.23	1.55	0.35	52
20.7.90	20	8.1	0.91	5.94	0.68	0.13	0.32	0.24	1.43	0.37	56
20.7.90	25										
20.7.90	50	5.5	1.06	6.06	0.90	0.16	0.37	0.28	1.61	0.41	79
15.8.90	1	12.3	0.91	6.19	0.67	0.13	0.33	0.24	1.35	0.37	39
15.8.90	6	11.8	0.88	6.16	0.73	0.13	0.32	0.23	1.37	0.37	39
15.8.90	10	10.2	0.88	6.17	0.79	0.13	0.33	0.23	1.40	0.33	48
15.8.90	15	8.7	0.92	6.07	0.83	0.13	0.33	0.26	1.42	0.37	56
15.8.90	20	7.8	0.95	6.00	0.80	0.13	0.33	0.24	1.46	0.37	57
15.8.90	50	6.5	1.08	5.93	0.93	0.15	0.36	0.28	1.67	0.41	61
15.8.90	55										
19.9.90	1	8.0	0.95	6.28	0.75	0.14	0.33	0.23	1.42	0.35	57
19.9.90	6	8.0	0.92	6.27	0.74	0.13	0.32	0.23	1.37	0.38	58
19.9.90	10	8.0	0.94	6.28	0.75	0.13	0.32	0.23	1.46	0.33	59
19.9.90	15	8.0	0.94	6.27	0.69	0.13	0.34	0.23	1.44	0.35	57
19.9.90	20	8.0	0.94	6.27	0.76	0.14	0.33	0.23	1.33	0.37	58
19.9.90	50	6.2	1.06	6.13	0.82	0.18	0.36	0.27	1.55	0.38	84
19.9.90	55										

Continued on p. 138

Annex 2. Continued.

Date	Depth (m)	Temp. (°C)	Cond. (mS m ⁻¹)	pH	Ca (mg l ⁻¹)	Mg (mg l ⁻¹)	Na (mg l ⁻¹)	K (mg l ⁻¹)	SO ₄ (mg l ⁻¹)	Cl (mg l ⁻¹)	NO ₃ -N (µg l ⁻¹)
11.6.91	1	6.0	1.10	6.34	0.92	0.16	0.38	0.28	1.62	0.41	76
11.6.91	6	5.7	1.05	6.30	0.92	0.16	0.38	0.29	1.69	0.37	74
11.6.91	10	5.8	1.05	6.34	0.93	0.15	0.38	0.29	1.69	0.42	74
11.6.91	15	5.8	1.05	6.30	0.91	0.15	0.38	0.28	1.65	0.41	76
11.6.91	20	5.5	1.05	6.31	0.88	0.15	0.39	0.29	1.64	0.38	81
11.6.91	50	4.8	1.05	6.28	0.88	0.15	0.38	0.28	1.65	0.41	65
11.6.91	55	4.8	1.05	6.26	0.88	0.15	0.38	0.29	1.62	0.39	87
9.7.91	1	14.5	0.99	6.18	0.75	0.13	0.36	0.26	1.50	0.46	63
9.7.91	6	8.9	0.94	6.12	0.74	0.13	0.33	0.26	1.54	0.38	68
9.7.91	10	7.5	0.94	6.03	0.80	0.13	0.33	0.26	1.63	0.35	72
9.7.91	15	6.5	0.99	6.09	0.82	0.14	0.35	0.28	1.60	0.39	75
9.7.91	20	5.9	0.99	6.12	0.84	0.14	0.36	0.27	1.59	0.39	78
9.7.91	50	5.7	1.05	6.20	0.90	0.15	0.37	0.28	1.64	0.41	84
9.7.91	55	5.7	1.05	6.18	0.89	0.15	0.37	0.28	1.61	0.41	81
31.7.91	1	16.8	0.88	6.25	0.73	0.12	0.32	0.23	1.38	0.37	54
31.7.91	6	11.9	0.88	6.18	0.75	0.12	0.32	0.24	1.42	0.39	64
31.7.91	10	10.4	0.88	6.13	0.73	0.12	0.31	0.23	1.41	0.37	69
31.7.91	15	8.6	0.94	6.13	0.79	0.13	0.33	0.26	1.48	0.39	73
31.7.91	20	7.0	0.99	6.15	0.85	0.14	0.35	0.26	1.52	0.42	77
31.7.91	25	6.9	0.99	6.12	0.86	0.14	0.36	0.28	1.67	0.33	79
31.7.91	55	5.7	1.05	6.13	0.92	0.15	0.36	0.28	1.59	0.43	83
25.8.91	1	12.4	0.88	6.28	0.74	0.12	0.32	0.22	1.46	0.30	37
25.8.91	6	12.0	0.88	6.26	0.75	0.12	0.34	0.25	1.42	0.33	40
25.8.91	10	11.0	0.88	6.17	0.76	0.12	0.32	0.23	1.42	0.35	50
25.8.91	15	8.7	0.94	6.11	0.80	0.13	0.33	0.25	1.53	0.37	73
25.8.91	20	7.7	0.99	6.13	0.85	0.14	0.35	0.27	1.55	0.42	80
25.8.91	50	6.0	1.05	6.16	0.90	0.14	0.37	0.28	1.69	0.35	86
25.8.91	55	6.0	1.05	6.16	0.97	0.16	0.41	0.31	1.62	0.40	86
29.9.91	1	6.8	0.94	6.29	0.85	0.13	0.35	0.26	1.52	0.38	65
29.9.91	6	6.8	0.99	6.29	0.86	0.14	0.36	0.27	1.62	0.33	64
29.9.91	10	6.8	1.05	6.26	0.84	0.13	0.35	0.26	1.48	0.40	49
29.9.91	15	6.8	0.99	6.28	0.85	0.14	0.36	0.26	1.57	0.33	67
29.9.91	20	6.8	0.99	6.28	0.85	0.14	0.36	0.27	1.57	0.36	61
29.9.91	50	5.8	1.05	6.11	0.92	0.14	0.36	0.28	1.61	0.38	85
29.9.91	55	5.7	1.05	6.09	0.91	0.14	0.36	0.27	1.60	0.38	87

Continued on p. 139

Annex 2. Continued.

Date	Depth (m)	Temp. (°C)	Cond. (mS m ⁻¹)	pH	Ca (mg l ⁻¹)	Mg (mg l ⁻¹)	Na (mg l ⁻¹)	K (mg l ⁻¹)	SO ₄ (mg l ⁻¹)	Cl (mg l ⁻¹)	NO ₃ -N (µg l ⁻¹)
9.6.92	1	12.0	0.94	5.99	0.62	0.12	0.42	0.28	1.05	0.59	53
9.6.92	6	8.3	0.89	5.97	0.61	0.12	0.39	0.27	1.15	0.54	76
9.6.92	10	5.8	0.94	5.95	0.67	0.13	0.40	0.31	1.17	0.57	88
9.6.92	15	4.6	0.99	6.02	0.77	0.14	0.41	0.33	1.32	0.52	82
9.6.92	20	5.0	1.01	6.08	0.83	0.15	0.41	0.33	1.39	0.46	81
9.6.92	50	3.8	1.05	6.12	0.88	0.16	0.41	0.32	1.50	0.46	85
9.6.92	55	3.7	1.06	6.15	0.86	0.17	0.41	0.33	1.38	0.43	87
4.7.92	1	10.0	0.94	6.16	0.72	0.15	0.41	0.29	1.24	0.48	52
4.7.92	6	9.0	0.96	6.11	0.72	0.14	0.40	0.29	1.21	0.54	56
4.7.92	10	8.4	0.97	6.02	0.74	0.15	0.40	0.30	1.27	0.48	61
4.7.92	15	6.8	1.00	6.06	0.80	0.15	0.41	0.31	1.27	0.50	72
4.7.92	20	6.6	1.00	6.08	0.78	0.15	0.40	0.31	1.37	0.46	77
4.7.92	50	5.8	1.01	6.09	0.82	0.15	0.41	0.32	1.39	0.46	80
4.7.92	55	5.5	1.02	6.00	0.83	0.16	0.41	0.32	1.40	0.44	77
7.8.92	1	11.5	0.92	6.30	0.71	0.14	0.39	0.27	1.26	0.41	38
7.8.92	6	11.1	0.92	6.25	0.72	0.14	0.39	0.26	1.20	0.43	39
7.8.92	10	10.3	0.94	5.93	0.74	0.14	0.38	0.28	1.35	0.41	5
7.8.92	15	8.5	0.98	6.13	0.75	0.14	0.40	0.29	1.23	0.48	65
7.8.92	20	7.0	0.98	6.26	0.79	0.16	0.40	0.30	1.33	0.46	74
7.8.92	25	5.0	1.02	6.07	0.85	0.16	0.41	0.32	1.35	0.48	88
7.8.92	55	5.0	1.01	6.07	0.83	0.16	0.40	0.31	1.41	0.46	75
11.9.92	1	8.3	0.90	6.17	1.05	0.16	0.37	0.25	1.23	0.43	57
11.9.92	6	8.3	0.90	6.16	0.74	0.14	0.37	0.25	1.21	0.41	61
11.9.92	10	8.3	0.90	6.18	0.71	0.13	0.37	0.25	1.23	0.41	60
11.9.92	15	8.1	0.90	6.14	0.76	0.14	0.38	0.26	1.22	0.43	59
11.9.92	20	8.0	0.90	6.12	0.73	0.13	0.38	0.25	1.20	0.42	64
11.9.92	50	5.1	1.03	6.02	0.84	0.15	0.41	0.31	1.30	0.46	92
11.9.92	55	5.0	1.02	6.03	0.83	0.15	0.41	0.31	1.32	0.46	92
3.10.92	1	6.8	0.90	6.22	0.76	0.14	0.38	0.25	1.24	0.41	70
3.10.92	6	6.8	0.90	6.22	0.75	0.13	0.38	0.25	1.24	0.43	72
3.10.92	10	6.8	0.90	6.21	0.81	0.16	0.43	0.30	1.25	0.41	72
3.10.92	15	6.8	0.89	6.19	0.73	0.14	0.38	0.25	1.26	0.43	67
3.10.92	20	6.7	0.90	6.16	0.75	0.14	0.37	0.25	1.26	0.41	77
3.10.92	50	5.0	1.02	6.01	0.83	0.15	0.41	0.30	1.42	0.48	103
3.10.92	55	5.0	1.02	5.99	0.83	0.15	0.41	0.30	1.38	0.43	95

Continued on p. 140

Annex 2. Continued.

Mean values, mg l ⁻¹									
Date	Cond. (mS m ⁻¹)	pH	Ca (mg l ⁻¹)	Mg (mg l ⁻¹)	Na (mg l ⁻¹)	K (mg l ⁻¹)	SO ₄ (mg l ⁻¹)	Cl (mg l ⁻¹)	NO ₃ -N (µg l ⁻¹)
1990	0.98	6.10	0.75	0.14	0.34	0.26	1.52	0.38	59.58
1991	0.99	6.20	0.84	0.14	0.36	0.27	1.57	0.38	70.96
1992	0.96	6.10	0.78	0.15	0.40	0.29	1.29	0.46	70.06
Mean values, µeq l ⁻¹									
Date	Ca (µeq l ⁻¹)	Mg (µeq l ⁻¹)	Na (µeq l ⁻¹)	K (µeq l ⁻¹)	Kat. (µeq l ⁻¹)	Alk. (µeq l ⁻¹)	SO ₄ (µeq l ⁻¹)	Cl (µeq l ⁻¹)	
1990	37.6	11.6	14.8	6.6	70.6	26.7	33.0	10.8	
1991	42.1	11.4	15.4	6.8	75.8	31.0	34.0	10.8	
1992	38.7	12.0	17.3	7.4	75.3	34.4	27.9	13.0	
Mean values. cation/anion per cent ratios									
Date	Ca (%)	Mg (%)	Na (%)	K (%)		Alk. (%)	SO ₄ (%)	Cl (%)	
1990	53.3	16.4	21.0	9.3		37.8	46.8	15.4	
1991	55.6	15.1	20.4	9.0		40.9	44.8	14.2	
1992	51.3	15.9	22.9	9.8		45.7	37.0	17.2	



The phytoplankton of Lake Atnsjøen, Norway – a long-term investigation

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Key words: phytoplankton, oligotrophy, long-term, species composition, biovolume, seasonal variations

Abstract

Quantitative samples were collected from Lake Atnsjøen five times per year in the growth seasons 1990–2000. The samples were analysed for variation in the phytoplankton composition, and the total volume and volume of the main groups of algae were calculated. Lake Atnsjøen is a large, deep and unregulated lake with a surface area of 4.8 km² and a maximum depth of 80.2 m. It is a nutrient-poor, oligotrophic lake with a maximum phytoplankton volume varying between 125–393 mm³/m³ in the years 1990–2000. The phytoplankton community is dominated by species of the groups Chrysophyceae and Cryptophyceae. The chrysophytes dominate the phytoplankton in the early part of the growth season (May–June) while the cryptophytes increase throughout the season and dominate in the autumn. Among the chrysophytes different species of chrysomonads were most frequent together with common species of the genus *Dinobryon* like *D. borgei*, *D. cylindricum* var. *alpinum* and *D. crenulatum*. A total of 22 species or taxa of chrysophytes were recorded in the samples. Common among the cryptomonads were several species of the genus *Cryptomonas*. Most important quantitatively, however, were *Rhodomonas lacustris* and *Katablepharis ovalis*. The succession of the phytoplankton throughout the growth season was similar from year to year in quantitative as well as qualitative terms, but some changes were recorded after the great flood in 1995. Canonical Correspondence Analysis (CCA) shows a slight, but significant, phytoplankton community change over the succeeding years.

Introduction

The importance of long-term limnological studies including all trophical levels in a pelagic system has been stressed by several investigators, (e.g. De Bernardi et al., 1988; Elliott, 1990; Gophen et al., 1990). Data series to demonstrate the natural annual variation must be obtained in lakes with minimum anthropogenic influence. Such lakes are often found in areas of high altitude, or in areas where most of the catchment of the lake is situated in the mountains. In such systems there is little variation in the nutrient content of the waters throughout the growth season. Most of the recorded variation, for instance in the phytoplankton community, is primarily related to variation in the

water discharge due to snow melting in the spring, or heavy rain.

The previously most complete investigation of a relatively pristine mountain lake in Norway, was done in the relatively shallow lake Øvre Heimdalsvatn in the Jotunheimen area, central southern Norway. Variation in the phytoplankton community of that lake was investigated by Brettum (1972) and Tangen & Brettum (1978). Quantitative samples of phytoplankton from Lake Atnsjøen have previously been collected in 1980 (Holtan et al., 1982), 1987 (Fagernes, 1989); and 1988 (Brettum, unpublished).

Atnsjøen has been selected as a reference lake where natural variation may be documented in a system with little influence by human activities. Phytoplankton biovolume and composition is one of the

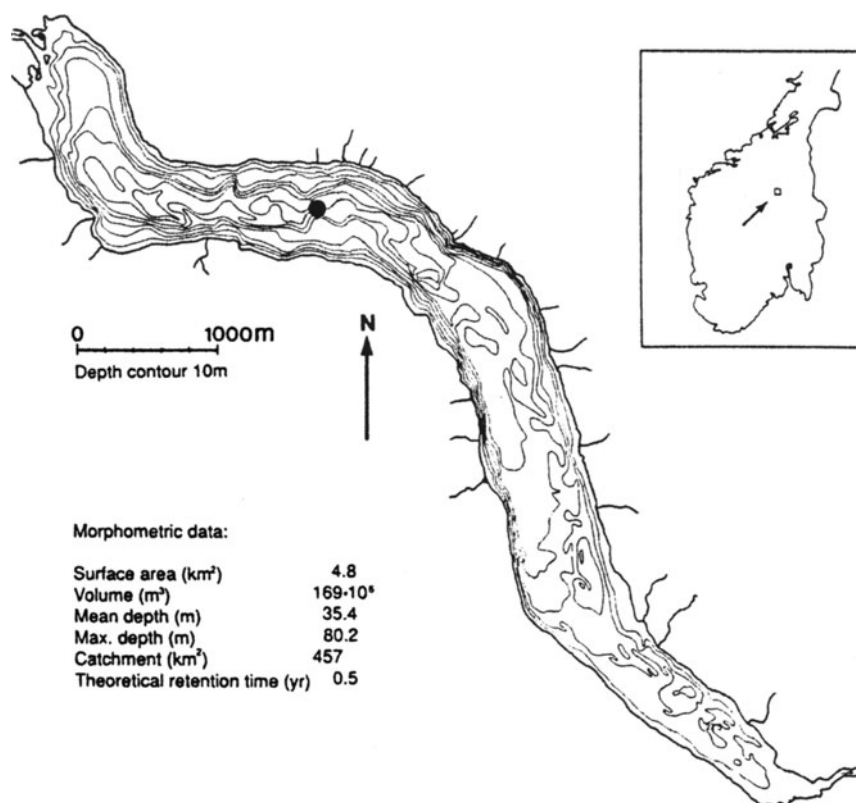


Figure 1. Location of Lake Atnsjøen, central part of southern Norway, with phytoplankton sampling locality indicated (from Fagernæs 1989).

central parameters in the pelagic ecosystem of lakes. It is therefore essential to record long-term in this parameter to understand the natural variation in the lake ecosystem.

The results reported in this paper cover the period 1990–2000, and demonstrate the natural variation in phytoplankton biovolume and composition of this large, deep, and unregulated lake.

The site

Lake Atnsjøen is the largest lake in the Atna water-course with a surface area of 4.8 km² and a volume of 169×10^6 m³. Maximum depth is 80.2 m and the mean depth 35 m. The theoretical retention time is 6 months. The lake is situated in the eastern, central part of southern Norway, at an altitude of 701 m a.s.l. The catchment area is 457 km² (Fig. 1), and approximately 88% of the catchment are mountain area above the forest limit. The lake and most of the catchment area are situated in a typical inland climatic zone, with a mean precipitation of 562 mm per year, most of it in

June–September. The area is usually poor in snow, and ice covers the lake from late October to the end of May (Nordli & Grimnes, 2003).

Lake Atnsjøen has an extremely low conductivity, usually between 0.8 and 1 mS m⁻¹, showing a poor content of ions in the water. The lake is slightly acid with a pH between 6.0 and 6.1, but in periods of snow melting in May–June it may decrease to 5.8, while in the summer period it may increase to 6.3. The buffer capacity is low with an alkalinity between 0.048 and 0.071 mmol l⁻¹. The content of humic substances is usually low. Water colour varies between 12 and 41 mg Pt/l, but is usually around 15–20 mg/l Pt. The content of particles is also low; the turbidity is usually between 0.2 and 0.8 FTU. Maximum turbidity is recorded in flood periods in the spring. This influences the Secchi disk depth, which is usually between 9 and 10 m, but may decrease to 4–5 m during the spring flood period.

The nutrient content is low with total phosphorus values between 4 and 5 µg/l P and total nitrogen usually between 120 and 200 µg/l N. This reflects an oligotrophic lake.

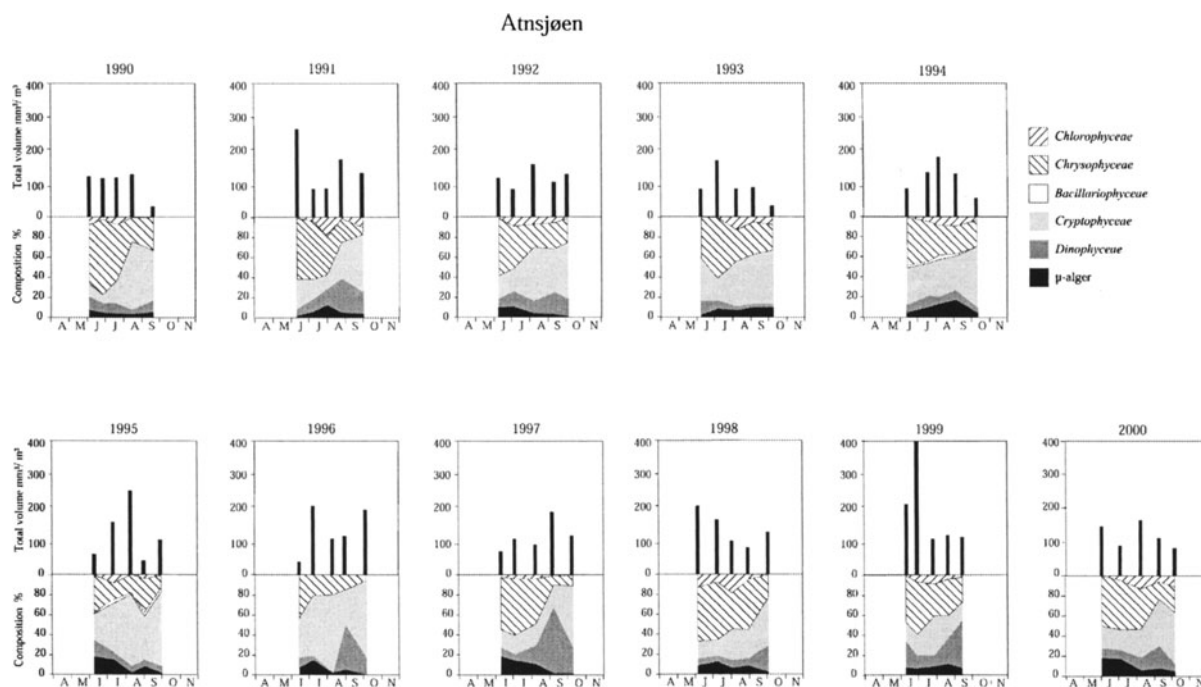


Figure 2. Variations in total volume and composition of phytoplankton in Lake Atnsjøen 1990–2000.

Material and methods

Quantitative phytoplankton samples were taken from the area over the deepest part of the lake five times every year in the period 1990–2000. The material consists of integrated samples from the surface to 10 m depth, collected with approximately equal intervals in the growth season from May to September/October each year. All samples were fixed and preserved with Lugol's solution added acetic acid.

The samples were examined according to Utermöhl (1958) and phytoplankton volume was calculated as recommended by Rott (1981). All the methods used for quantitative examination of phytoplankton are revised for use in the Nordic countries by Olrik et al. (1998). Chambers of 10 and 50 ml were used for the sedimentation procedure, and 2 to 4 transects examined.

The different species of phytoplankton were counted by means of an inverted microscope, Leitz Fluovert FS, with phase contrast. Large species were counted from the whole sedimentation area. A number of cells of each species were measured and the mean cell volume calculated, comparing the form of the species with simple geometric figures (Rott, 1981, Olrik et al., 1998). Phytoplankton volumes as volume of each species, the main groups (green algae, dinoflagellates,

etc.), and the total volume, were then calculated from each sample.

The confidence interval for mean number of individuals was $\pm 2 \times 100 / \sqrt{n} \%$, where n = number of individuals counted. To obtain a statistically acceptable estimate for the number of individuals of each species in the sample, a bottom area of the sedimentation chamber, containing at least 100 individuals for the important species, was examined. At least 500 individuals for the whole community of phytoplankton were counted in each sample (Lund et al., 1958, Venrick, 1978, Olrik et al., 1998).

Changes in the species composition of the phytoplankton community were analysed by canonical correspondence analysis (CCA; Ter Braak, 1986), an ordination method which has been shown to have superior properties with respect to aligning community changes to observed environmental gradients (Palmer, 1993). Biovolume estimates on 35 phytoplankton taxa occurring in 5 or more of the 45 samples through the years 1990–2000 were used in the CCA analysis. Biovolumes were square root transformed before analysis in order to stabilize variances (Hessen et al., 1995). Since the analysis was focused on temporal trends, the environmental gradient variables consisted only of time (decimal years: 1990 to 2000) and season (day of year: 1 to 365). Both linear and quadratic

Table 1. Recorded maximum and mean of phytoplankton for the growth seasons 1990–2000 in Lake Atnsjøen. All values in $\text{mm}^3 \text{m}^{-3}$.

Year	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
Maximum	125	260	156	165	180	245	203	184	199	393	165
Mean	100	145	117	91	117	120	130	113	131	185	119

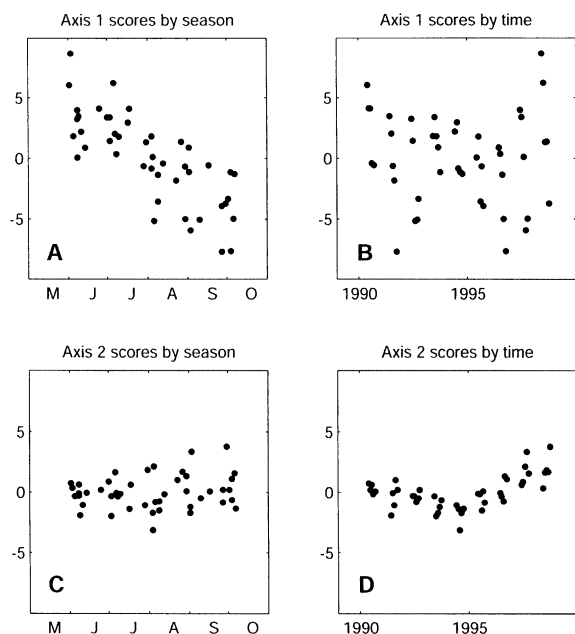


Figure 3. Sample scores on CCA axis 1 (A,B) and CCA axis 2 (C,D) plotted against season (A,C) and time (B,D). Sample scores are computed as averages of phytoplankton species abundances weighted by loading factors corresponding to the species coordinates in Fig. 4 (WA-scores, sensu McCune 1997).

functions of time and season were included in order to identify possible nonlinearities.

Results and discussion

Two main groups of phytoplankton dominated the community of phytoplankton throughout the growth seasons all years (Fig. 2). These were the chrysophytes (Chrysophyceae) and the cryptomonads (Cryptophyceae). Some years, the dinoflagellates (Dinophyceae) were more frequent and constituted a more dominant part of the total phytoplankton community in early autumn (August–September). The total volume is given as $\text{mm}^3 \text{m}^{-3}$, which is approximately the same as mg m^{-3} of fresh weight phytoplankton. Fig. 2 compiles the results from all the samples taken from the main station in Lake Atnsjøen in the

years 1990–2000. The chrysophytes were dominating in the early part of the growth season (i.e. June–July), while the volume of cryptomonads usually increased throughout the season (Fig. 2), playing a dominant role in the autumn.

Other main groups of phytoplankton were of minor quantitative importance, even though species of the green algae (Chlorophyceae) were frequent in the phytoplankton community in the summer period. As is often the case in oligotrophic waters, the group ‘ μ -algae’ containing small indetermined forms with a diameter of 2–4 μm , was occasionally an important part of the total phytoplankton community. Diatom species (Bacillariophyceae) were hardly recorded in the samples, and they were of no importance in terms of abundance at any time throughout the whole period of investigation. The total volume of phytoplankton in the waters of Lake Atnsjøen was rather low both in terms of growth season mean as well as recorded maximum (Table 1).

A total of 22 species or taxa of chrysophytes were recorded in the samples. Different species and forms of chrysomonads were most frequent and constituted the major part of this group. Common, but not frequent, species among the chrysophytes were *Dinobryon borgei*, *D. cylindricum* var. *alpinum*, and *D. crenulatum* besides a species of the genus *Chromulina*, probably *C. pseudonebulosa*.

The cryptomonads were dominated by several species of the genus *Cryptomonas* among them *Cryptomonas* cf. *erosa*, *C. erosa* var. *reflexa* (*C. reflexa* ?), and *C. marssonii*. Most of the volume of this group was, however, made up by *Katablepharis ovalis* and particularly *Rhodomonas lacustris*. These two species are very common in most lake types in all parts of Norway. However, they become less frequent in the phytoplankton community as the pH decreases below 5.5, and disappear completely in lakes with a pH below 5.0 (Brettum 1989). Thus, they are excellent indicator species for acidity as well as in the process of restoration of the biotic society in acidified lakes by liming.

Table 2. Species of phytoplankton frequently found in Lake Atnsjøen.

Cyanophyta	Bacillariophyceae
Cyanophyceae	<i>Asterionella formosa</i> Hassall
<i>Planktothrix mougeotii</i> Anagnostis et Komárek	<i>Aulacoseira alpigena</i> (Grunow) Krammer
	<i>Cyclotella radiosa</i> (Grunow) Lemmermann
	<i>Fragilaria ulna</i> (morphotyp 'ulna') (Nitzsch) Lange-Bertalot
	<i>Tabellaria flocculosa</i> (Roth) Kützing
Chlorophyta	Cryptophyta
<i>Ankistrodesmus falcatus</i> (Corda) Ralfs	Cryptophyceae
<i>Ankyra lanceolata</i> (Korshikov) Fott	<i>Chroomonas</i> sp.
<i>Botryococcus braunii</i> Kützing	<i>Cryptomonas erosa</i> Ehrenberg
<i>Carteria</i> sp.	<i>Cryptomonas erosa</i> var. <i>reflexa</i> Marsson
<i>Chlamydomonas</i> spp.	<i>Cryptomonas marssonii</i> Skuja
<i>Crucigenia quadrata</i> Morren	<i>Cryptomonas</i> spp.
<i>Crucigeniella rectangularis</i> (Nägeli) Komárek	<i>Katablepharis ovalis</i> Skuja
<i>Dictyosphaerium pulcellum</i> var. <i>minutum</i>	<i>Rhodomonas lacustris</i> Pascher et Ruttner
Deflandre	Dinophyta
<i>Dictyosphaerium subsolitarium</i> van Goor	Dinophyceae
<i>Elakatothrix genevensis</i> (Reverdin) Hindák	<i>Amphidinium</i> sp.
<i>Koliella</i> sp.	<i>Gymnodinium</i> cf. <i>uberrimum</i> (Allman)
<i>Oocystis marssonii</i> Lemmermann	Kofoed et Swezy
<i>Oocystis rhomboidea</i> Fott	<i>Gymnodinium</i> sp.
<i>Oocystis submarina</i> var. <i>variabilis</i> Skuja	<i>Peridinium</i> sp.
<i>Selenastrum capricornutum</i> Printz	<i>Peridinium umbonatum</i> Stein
<i>Sphaerocystis Schroeteri</i> Chodat	<i>Peridinium willei</i> Huitfeld-Kaas
Indet.coccoid green algae	Indet.dinoflagellate
Chrysophyta	Xanthophyceae
Chrysophyceae	<i>Isthmochloron trispinatum</i> (W. et G.S.West)
<i>Bitrichia chodatii</i> (Reverdin) Hollande	Skuja
<i>Chromulina</i> cf. <i>pseudonebulosa</i> Pascher	<i>Tetraëdriella patiens</i> Ramberg
<i>Chrysococcus</i> sp.	
<i>Chrysolykos skujai</i> (Nauwerck) Bourrelly	
Craspedomonads	
<i>Dinobryon borgei</i> Lemmermann	
<i>Dinobryon crenulatum</i> W. et G.S. West	
<i>Dinobryon cylindricum</i> var. <i>alpinum</i>	
(Imhof) Bachmann	
<i>Dinobryon korshikovii</i> Matvienko	
<i>Kephyrion boreale</i> Skuja	
<i>Kephyrion</i> sp.	
<i>Mallomonas akrokomos</i> Ruttner	
<i>Mallomonas</i> spp.	
<i>Ochromonas</i> spp.	
Small chrysomonads (d < 7 µm)	
Large chrysomonads (d > 7 µm)	
<i>Spiniferomonas</i> sp.	

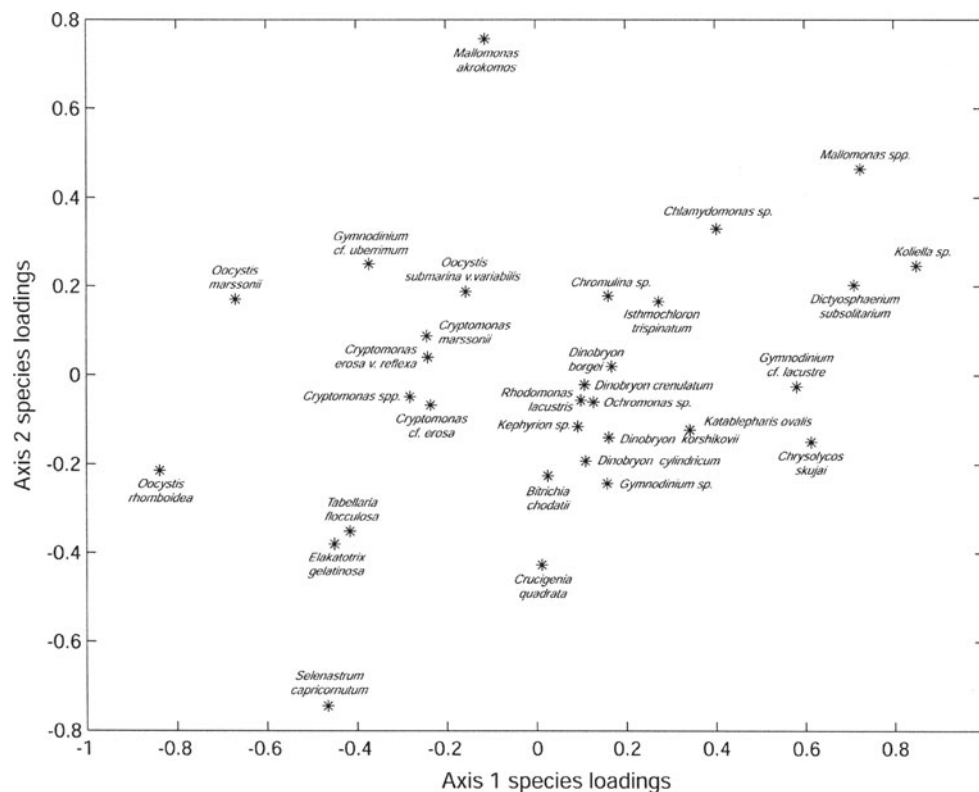


Figure 4. Ordination diagram constructed from the two first axes of a canonical correspondence analysis on square root transformed biovolumes of the 35 species of phytoplankton that were recorded in more than 5 samples.

In the years when the proportion of dinoflagellates increased markedly in the autumn, the dominant species belonged to the genus *Gymnodinium* (*G. lacustre* and *G. cf. uberrimum*). Because only fixed material was available, the identification of species in this genus, particularly *G. uberrimum*, may be uncertain. The species *Peridinium umbonatum* (earlier *P. inconspicuum*), very common in smaller and more acid and humic waters (Brettum, 1989), was only recorded with a few individuals in some of the samples from Lake Atnsjøen.

Twenty different species of green algae were recorded in the samples, but they were usually of little quantitative importance. The only species that occasionally occurred in significant numbers were *Crucigenia quadrata* and *Oocystis submarina* var. *variabilis*. Among the diatoms, only two species occurred in any significant number, i.e. *Tabellaria flocculosa* and *Aulacoseira alpigena*.

Permutation tests in the CCA-analysis showed that all the first three CCA axes were highly significant ($p < 0.0025$), while the fourth axis was not ($p =$

0.075). By plotting sample scores (WA-scores, sensu McCune 1997) against time and season (Fig. 3), it appears that CCA axis 1 represents the seasonal succession while CCA axis 2 is more representative of the long-term changes in community structure. Comparing this with the corresponding species ordination diagram (Fig. 4), indicates that seasonal succession proceeds from right to left along CCA axis 1, while the long-term trend implies a displacement from bottom to top along CCA axis 2. Several of the dominant contributors to total phytoplankton volume, such as the cryptomonads and the *Dinobryon* species, are located close to the origin of the ordination diagram, reflecting their ubiquitous presence and lack of temporal pattern. The typical seasonal succession seems to proceed from a spring community characterized by *Koliella* sp., *Dictyosphaerium subsolitarium*, *Gymnodinium cf. lacustre*, *Chrysolykos skujai*, and several *Mallomonas* species to an autumn community characterized by several *Oocystis* species. The long-term trend appears to involve a community change towards decreasing occurrence of several chlorococcal species (*Selenastrum*

capricornutum, *Crucigenia quadrata*, and *Elakatotrix gelatinosa*) in favour of an increasing importance of *Mallomonas* species. The reason for this apparent long-term trend remains unknown, but it should be noticed that the sharp breakpoint in CCA axis 2 scores occur in 1995, which was a year with a unusually large flood (Tvede, 2003). It is possible that the repercussions of this event, perhaps in terms of increased transport of particles and particle-bound nutrients, are reflected in the slight, but significant, phytoplankton community changes over the succeeding years.

Acknowledgements

We would like to thank Tom Andersen (Norwegian Institute for Water Research) for assistance with the CCA-analysis of the material. The investigations were funded by the State Pollution Control Authority (SFT), the Directorate for Nature Management (DN), and the Norwegian Water Resources and Energy Directorate (NVE).

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Zooplankton in Lake Atnsjøen 1985–1997

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Key words: Lake, zooplankton, Rotatoria, Copepoda, Cladocera, life cycles

Abstract

The aim of this paper is to study long-term changes in the zooplankton of a subalpine locality unaffected by direct anthropogenic disturbances. The material has been collected during the period 1985–1997; since 1988 a standardised sampling program has been followed, with five sampling dates during the ice free period (June–October) at three fixed stations. Altogether 17 species of Rotatoria, 9 species of Copepoda and 11 species of Cladocera were recorded. Of these 10 species of Rotatoria, two species of Copepoda and five species of Cladocera occur regularly in the plankton. *Polyarthra vulgaris* dominate among the rotifers together with *Kellicottia longispina* and *Conochilus unicornis*. The crustacean community is dominated by the copepod *Cyclops scutifer*, and the cladocerans *Bosmina longispina*, *Holopedium gibberum* and *Daphnia longispina*. The cladocerans *Bythotrephes longimanus*, *Polyphemus pediculus*, and the copepods *Arctodiaptomus laticeps* and *Heterocope saliens* all occur regularly, but at low densities. The zooplankton density is low in May/June and peaks in August and September, but the timing of maximum densities varies from year to year. By numbers, the rotifers strongly dominate with densities 10–15 times higher than the crustaceans. The annual maximum density (rotifers plus crustaceans) ranged from 50 ind. l⁻¹ (1985, 1988) to 450 ind. l⁻¹ (1995). Mean density is about 140–150 ind. l⁻¹. By biomass (dry weight), the cladocerans constitute 60%, while the copepods and rotifers constitute 30% and 10% of the zooplankton, respectively. The annual maximum has varied between 70 and 260 µg dw l⁻¹, with 170 µg dw l⁻¹ as the mean level. *C. scutifer* usually has a one-year lifecycle without diapause, but a small fraction of the population has a two-year lifecycle. The life cycle in 1989 and 1990 differed strongly from the other years. The life cycles of *B. longispina*, *D. longispina* and possibly also *H. gibberum* and *A. laticeps*, indicate two generations during the summer. *H. gibberum* and *H. saliens* pass the winter as resting eggs. The other crustacean species, except *C. scutifer*, pass the winter mainly as resting eggs, but all have a small winter population in the water mass. *C. scutifer* is the only species without resting eggs. The vertical distribution normally shows highest density between 5 and 10 m depth. However, during some periods maximum density is observed close to the surface, while at other times it is seen deep in the hypolimnion. The vertical distribution is most pronounced when the thermocline is sharp, and less pronounced during the full circulation in autumn. The vertical migration may also be pronounced, especially in *B. longispina*, with high density near the surface during the night. The vertical migration is less pronounced among the rotifers and copepods. The degree of vertical migration varies with temperature and food conditions. There is little variation from year to year in species composition, but large variation in species dominance, seasonal development, population density, and vertical and horizontal distribution during the sampling period. Variations in temperature, food condition, predation, and water through-flow are possible causes for the observed differences between the years. Input of allochthonous material is especially important. However, no clear correlation have been found between the development of the plankton community and these environmental factors. Hence, these interactions are complex and multifactorial.

Introduction

A number of physical, chemical and biological factors influence the zooplankton community. The interaction between them are complicated, and the relative

importance of the factors varies both seasonally and between years. Normally, it is therefore difficult to identify the most important factors at any time, and the impact of individual factors may only be detected under extreme conditions. The high flood in May/June

1995 demonstrated in an impressive way the importance of allochthonous material for the zooplankton community in Lake Atnsjøen (Brabrand, 1998). The zooplankton density increased three-fold and the biomass two-fold after the flood, compared with earlier years.

A common feature of most natural ecosystems is the pronounced variation in space and time. In order to separate natural variations from impacts of human interventions, we need to understand the natural variation in time and space. This understanding can only be achieved by analysing long term data sets. Long-term studies are important in relation to the effects of e.g. climatic changes, acid precipitation, eutrophication, and hydropower regulation of rivers and lakes.

Most zooplankton studies are restricted in time, and they are consequently not well suited for understanding the long-term development and variation in zooplankton communities. Most time series data concern localities under significant anthropogenic influence, such as Lake Mjøsa, where the zooplankton has been monitored in relation to the eutrophication of the lake over the last 30 years (Kjellberg, 1999). Long-term changes in the zooplankton community of Lake Jonsvatn were monitored from 1977 to 1994 after the introduction of *Mysis relicta* (Koksvik & Reinertsen, 1995). Among the non-disturbed lakes, one of the most extensively studied ecosystems in Norway is the subalpine Lake Øvre Heimdalsvatn, which was studied for five years during the IBP period (1969–1973; Larsson et al., 1978).

This study was started in 1985 (Dervo, 1988; Dervo et al., 1991), and includes the long-term variation in species composition, as well as the population dynamics of the main species in the zooplankton community of the Lake Atnsjøen. Previous information about the zooplankton in Lake Atnsjøen is scarce (Matzow, 1974; Eie, 1982; Holtan, 1982).

Lake Atnsjøen and its catchment area

The geographic position, geology and hydrology

The oligotrophic and dimictic Lake Atnsjøen, with an area of 4.8 km², is the largest lake in the River Atna watershed. It is situated 701 m a.s.l., and has a catchment area of 457 km² of which 85% is situated above 1000 m a.s.l., which corresponds to the treeline in this area. The maximum and mean depths

are 80 m and 35.4 m, respectively, and the lake volume is $169 \cdot 10^6$ m³ (Holtan et al., 1982; Østrem et al., 1984) (Fig. 1). The theoretical retention time is short, about 6 months, and during the high flood in 1995 the retention time was reduced to only eleven days (Halvorsen, 2004). The hydrology of the catchment area is described by Tvede (2004).

The mean discharge at the outlet of Lake Atnsjøen is 10.0 m³ s⁻¹, varying from about 2–3 m³ s⁻¹ during winter, and exceeding 50 m³ s⁻¹ during short periods in summer. The spring flood occur in May and the first part of June, while there are normally no pronounced floods during autumn. The spring flood in 1995 was extreme with the water flow increasing from about 6 m³ s⁻¹ on 25 May to 182 m³ s⁻¹ on 1 June, and subsequently decreasing to about 80 m³ s⁻¹ on 5 June (Tvede, 2004).

The geology of the catchment area is uniform, and consists mainly of feldspar quartzite (sparagmite) (Oftedahl, 1950). The area has locally large deposits of Quaternary and fluvial materials (Bogen, 2004). There are no glaciers in the catchment area, but during cool summers permanent snow does occur, influencing the water temperature of both river and lake (Tvede, 2004).

The chemical weathering is slow, and the water's ion content is very low (Blakar, 1994; Halvorsen, 2004). The buffer capacity of the lakewater is low, with an alkalinity of less than 50 µeq l⁻¹ HCO₃; and a specific conductivity of 0.8–1.2 mS m⁻¹. The watershed is little affected by human activities, and the lake and the catchment area are therefore well suited for long-term studies of natural variation.

Climate

Lake Atnsjøen is situated in an area with a continental climate. The precipitation is highest during summer, from June to October, while the winter precipitation is low. The area is covered with snow from November to the beginning of May (Nordli & Grimnes, 2004). Over the sampling period, the mean yearly temperature has varied between -0.5 °C (1985) and 2.6 °C (1990), which is 1.2 °C below, and 1.9 °C above, the normal (Table 1). The mean annual precipitation is 555 mm; over the sampling period it has varied between 508 mm in 1989 and 673 mm in 1988.

Lake Atnsjøen is covered with ice from late November to late May (Tvede, 2004). During the sampling years, the ice-free period has varied between 165 days (1992/93) and 203 days (1989/90), with a

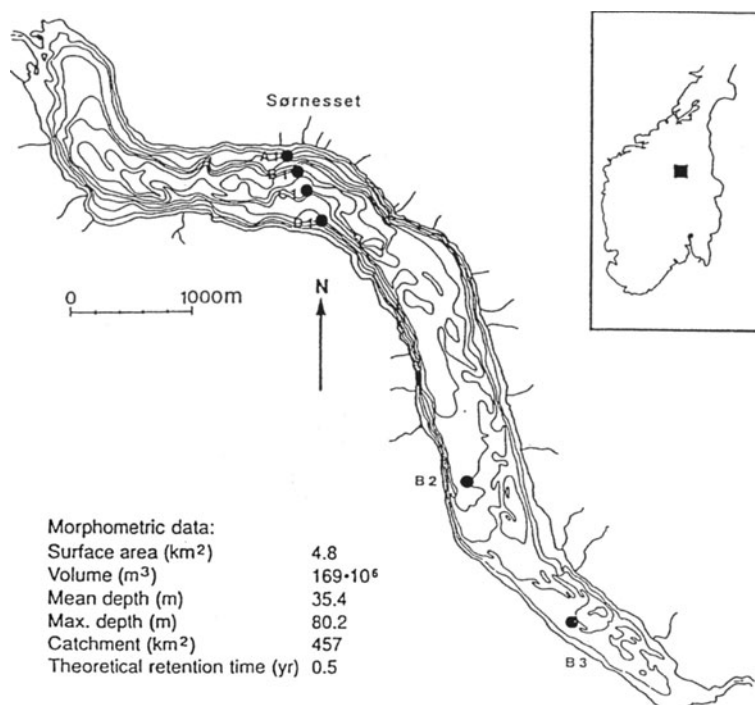


Figure 1. Depth contour map of Lake Atnsjøen with sampling stations. Depth contour line: 10 m

Table 1. Yearly precipitation (mm), and mean yearly temperature at Sørnesset compared with the mean of the normal periods 1931–1960 and 1961–90. The mean temperature for the period May–October (Mean, M–O) is also given together with the length of the ice free period (Sources: Norwegian Meteorological Institute; Nordli & Grimenes, 2004; Tvede, 2004). Depart. = departure from the normal.

	Temperature, °C		Temperature, °C		Precipitation, mm		Ice free period, days	
	Mean, year	Depart.	Mean, M-O	Depart.	Year	Depart.	Year	Depart.
1931–60	0.8		7.5		562			
1961–90	0.7		7.4		555		184	
1985	–0.6	–1.3	7.6	0.2	626	71	176	–8
1986	0.3	–0.4	7.5	0.1	541	–14	178	–6
1987	–0.1	–0.8	6.7	–0.7	578	23	181	–3
1988	1.5	0.8	8.3	0.9	673	118	177	–7
1989	2.3	1.7	7.5	0.1	508	–47	201	17
1990	2.6	1.9	8.0	0.6	564	9	203	19
1991	1.4	0.7	7.3	–0.1	542	–13	193	9
1992	1.8	1.1	7.0	–0.4	562	7	177	–7
1993	0.6	–0.1	6.1	–1.3	565	10	165	–19
1994	0.8	0.1	7.3	–0.1	547	–8	174	–10
1995	1.2	0.5	8.1	0.7	512	–43	183	–1
1996	–0.3	–1.0	7.3	–0.1	491	–64	168	–16
1997	1.7	1.0	8.4	1.0	462	–93	175	–9

mean of 184 days (Table 1). This corresponds approximately to the growing season of both phyto- and zooplankton. In Table 1 the mean air temperatures for the period May to October are compared with the 30-year normal (1961–90) for the same period. In seven out of 13 years the temperature have been at or above the normal, with maxima in 1988 and 1997. The coldest year was 1993, causing the water temperature not to exceed 10.3 °C (Halvorsen, 2004).

Water temperature

Lake Atnsjøen is weakly stratified during summer with a thermocline usually between 10 and 15 m in August (Halvorsen, 2004; Tvede, 2004). During the study period, the water temperature has varied by about 2 °C at 50 m depth and by as much as 6–8 °C at 1 m depth.

The surface temperature in summer normally varies between 10 and 14 °C, whereas the temperature in the hypolimnion varies between 3 and 6 °C. The highest temperatures, 16.8 °C and 17.5 °C, were measured at 1 m at the end of July 1991 and in the beginning of August 1994, respectively. The lowest maximum temperature, 10.3 °C, was measured in the beginning of August 1993 (Halvorsen, 2004; Tvede, 2004).

Secchi disk transparency and water colour

The Secchi disk transparency has varied between 4.3 m and 14.5 m, with highest visibility in autumn and lowest in spring and early summer (Halvorsen, 2004). The low transparency during spring and early summer is correlated with high water-flow and high input of allochthonous material. The blooming of phytoplankton is of less importance, and there is only a weak negative correlation between transparency and the density of zooplankton (Halvorsen, 2004).

The water colour, as read against the Secchi disk at the half transparency depth, normally varies between green and yellowish green, which are typical for oligotrophic lakes with none or only a small influence of humic substances (Strøm, 1943; Halvorsen, 2004). Only in exceptional cases a greenish yellow colour was observed, indicating a somewhat higher phytoplankton productivity.

Water chemistry

Lake Atnsjøen is extremely poor in electrolytes, with a specific conductivity normally lower than 1 mS m⁻¹ (Blakar, 1994; Halvorsen, 2004). Ca and SO₄ are the dominating ions. The Ca-content vary around

0.8 mg l⁻¹ while the SO₄ content is lower than 1.5 mg l⁻¹. There are no or only a slight chemical stratification in the lake.

The oxygen conditions are typical for oligotrophic lakes with short renewal time. At the end of the summer stagnation period the saturation is still high and normally higher than 80% in the profundal zone (Dervo, 1988).

Biological factors

The littoral zone in Lake Atnsjøen is steep, which reduce the extension of the vegetation zone. The water vegetation is mainly restricted to the depth interval between 2 and 5 m, and is dominated by quillwort (*Isoëtes lacustris*). The upper 2 m are wind and ice exposed and consist mostly of stones and gravel. According to the Secchi disk transparency the photogenic zone extends to about 30 m depth during summer (cf. Jónasson et al., 1992). During spring the compensation depth is higher because of high turbidity caused by large input of allochthonous material.

The phytoplankton is dominated by small species, less than 20 µm, and the total biomass is also low, normally less than 0.3 mm³ l⁻¹ (Brettum & Halvorsen, 2004). Chrysophyceae and Cryptophyceae dominate while Chlorophyceae occur regularly but in small numbers. Bacillariophyceae is hardly recorded. The species composition and biomass are typical for oligotrophic, high altitude lakes (Holtan, 1982; Dervo, 1988; Fagernæs, 1989; Brettum & Halvorsen, 2004).

The bottom fauna clearly reflects the oligotrophic character of the lake even if the fauna near the inlet river delta have some mesotrophic features (Aagaard et al., 1997).

The structure of the zooplankton community is heavily influenced by fish (Brooks & Dodson, 1965; Dervo, 1988; Saksgård & Hesthagen, 2004). In Lake Atnsjøen four species of fish occur, Arctic charr (*Salvelinus alpinus*), Brown trout (*Salmo trutta*), Alpine bullhead (*Cottus poecilopus*) and European minnow (*Phoxinus phoxinus*) (Hegge, 1988, 1991; Hesthagen et al., 2004). Bullhead, a few minnow, and small specimens of charr and trout (<230 mm) lives in the littoral zone down to 10 m depth. Larger individuals of charr and trout (230–330 mm) coexist in the pelagic zone. The charr is 3–4 times more numerous than the trout. Both species occur in highest density in the upper 2–3 m, but charr also occur down to 12 m depth (Hegge, 1988). Both species utilise crustacean zooplankton as food (Saksgård & Hesthagen, 2004).

Material and methods

The zooplankton material was sampled at three stations across the lake near Sørnesset (B1, C1 and D1 in Fig. 1). Until 1989 samples were also taken at three other stations along the lake (A1, B2 and B3 in Fig. 1).

Samples were taken 5 times each year during the ice-free period, from June to October. In 1986, material was sampled only three times, and in 1987 and 1988 four times. Sampling five times during the ice-free period is sufficient to describe the main dynamics in the community, and the lifecycle of the most numerous species.

The quantitative sampling of the zooplankton was done with three different samplers: a 3-liter Friedinger sampler in 1985, 1986 and 1987; a 2-liter Ruttner sampler partly used in 1987; and a 14-liter Schindler sampler used since 1988. The differences in sampling efficiency between these samplers are usually small (Bottrell et al., 1976; Larsson, 1978) but Langeland & Rognerud (1974) found distinct differences between Schindler and Friedinger samplers, and the density of both *Daphnia* spp. and *Eudiaptomus gracilis* were underestimated using the Friedinger sampler. We will assume, however, that the material from the different years may be compared.

The quantitative samples were filtered through a 45 µm mesh, which is small enough to retain all or most of the species and instars of the species (Larsson, 1978; Antonsson, 1992). Nevertheless, the large and fast swimming species such as *Bythotrephes longimanus*, *Arctodiaptomus laticeps* and *Heterocope saliens* seems to be a little underrepresented in the material (Dervo, 1988).

The sampling program has been standardised since 1988, and include samples from 0, 1, 2, 4, 6, 8, 10, 15, 20, 30 and 50 m. Until 1987 two parallel samples per depth were taken at all stations. Since 1988 5 samples per depth were taken at station B1 and two samples per depth at stations C1 and D1. This number of parallel samples may be a little too low, but as the coefficient of variation usually is lower than 5%, the results are considered acceptable (cf. Larsson, 1978; Antonsson, 1992). The variation is greater in summer and early autumn than in late autumn, probably because the absence of temperature stratification in late autumn. In addition, qualitative zooplankton samples were taken at each station with two parallel plankton net hauls from 20 m. The net diameter was 27 cm, the length 1 m, and the mesh size 45 µm. All plankton samples were preserved using a standard Lugol's solution.

All individuals in the quantitative zooplankton samples were counted while the qualitative samples were used as a supplement to ensure identification of rare species. The quantitative samples provide the density at each depth and mean population density at each sampling station. The mean density estimates were adjusted for the relative contribution of each depth interval (Larsson, 1978; Antonsson, 1992). Vertical and horizontal migrations increase the bias in estimating the population density in zooplankton. The horizontal differences are quite small in Lake Atnsjøen while the vertical diurnal migration may be pronounced (Dervo & Halvorsen, 1989). To obtain the best estimates of mean density and biomass, samples were taken at a certain time of the day. The high number of sampling depths in the epilimnion and upper hypolimnion contribute to reduce the effect of vertical migration on the results.

Zooplankton density is given as number of individuals per litre ($n\ l^{-1}$) or as biomass dry weight per litre ($\mu g\ dw\ l^{-1}$). Multiplying with the constant 35 400 yields density per m^2 . Thus $100\ ind.\ l^{-1}$ correspond to $3.5 \cdot 10^6\ ind.\ m^{-2}$.

The rotifers were counted and classified to species, or in some instances only to genus using Pontin (1978) and Ruttner-Kolisko (1972). The cladocerans and copepods were identified to species according to Flössner (1972, 2000), Sars (1903, 1918), Rylov (1948) and Kiefer (1973, 1978). The cladocerans were recorded as juveniles, females with and without eggs, and males, while the copepods were counted as nauplii, copepodite stages (Cop I–Cop V), females with and without eggs, and males. The number of eggs per female were also recorded. In copepods the nauplii were not identified to species, but the majority belongs to *Cyclops scutifer*.

The Shannon–Wiener diversity index (H') is calculated according to the formula $H' = -\sum (p_i)(\ln p_i)$ where S is number of species and p_i is the proportion of the i th species to the total number of individuals.

The biomass was calculated using formulas in Bottrell et al. (1976). Normally more than 50 specimens were measured according to standard procedures.

In order to identify the structural variation and similarities in the zooplankton community the data were analysed by means of detrended correspondence analyses (DCA) (Ter Braak, 1998). As the axes were short the principal components analyses (PCA) were also done. The total material, mean species densities ($n\ l^{-1}$) at each depth from each station, and sampling dates from the years 1989–1997, altogether

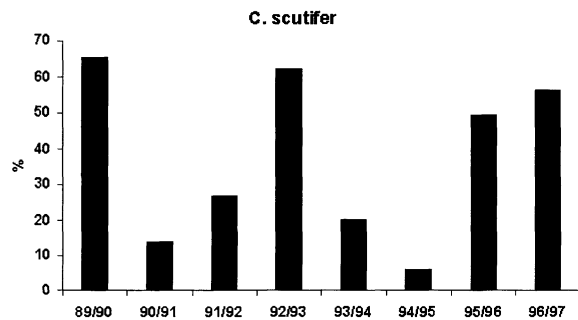


Figure 2. Percentage survival of *Cyclops scutifer* in Lake Atnsjøen during the winter season.

1246 samples, were used as input in this ordination. The environmental factors used in the correlation to the two main axes in the DCA and PCA analyses were water temperature, length of growing season (ice free period), number of degree days above 4 and 7 °C, respectively (measured at the outlet) (Tvede, 2004), precipitation and water discharge correlated to the loss of individuals through the outlet, and input of allochthonous material (Bogen, 2004). As fish is known to be one of the main structuring factors of the plankton community we also included the population size of the two main fish species, charr and trout (Hesthagen et al., 2004).

Results

Species composition

Altogether 37 species have been recorded; 17 species of rotifers, 9 species of copepods, and 11 species of cladocerans (Table 2). Of these 12 are considered littoral species, four are intermediate plankton-littoral species, while the remaining 21 species are pelagic zooplankton. Only 10 rotifer species, two copepod species and five cladoceran species occur regularly. The species composition have been quite constant throughout the study period.

The rotifer community was dominated by *Polyarthra vulgaris*, *Kellicottia longispina*, and *Conochilus unicornis*, while *Keratella hiemalis*, *K. cochlearis*, *Collotheca mutabilis*, and *Synchaeta pectinata* also did occur in quite high numbers. *Polyarthra remata* and *Asplanchna priodonta* were found regularly in low densities.

Among the crustaceans *Cyclops scutifer* and *Bosmina longispina* dominated while *Holopedium gibberum*, *Daphnia longispina* and *Arctodiaptomus*

Table 2. Species of Rotatoria, Copepoda and Cladocera occurring in Lake Atnsjøen during the period 1985–1997. Percentage occurrence in the total material of rotifers and crustaceans, respectively. P: planktonic, L: Littoral, PL: plankton-littoral, r: rare.

Species	Occurrence	Habitat
Rotatoria		
1 <i>Kellicottia longispina</i> (Kellicott)	24.4	P
2 <i>Keratella cochlearis</i> (Gosse)	4.6	P
3 <i>K. hiemalis</i> Carlin	3.9	P
4 <i>K. serrulata</i> (Ehrb.)	r	P
5 <i>Lepadella</i> sp.	r	L
6 <i>Lecane</i> sp.	r	L
7 <i>Trichocerca longiseta</i> (Schrank)	r	P
8 <i>Ascomorpha</i> sp.	r	P
9 <i>Polyarthra dolichopthera</i> Idelson	r	P
10 <i>P. remata</i> Skorikov	1.2	P
11 <i>P. vulgaris</i> Carlin	52.6	P
12 <i>Synchaeta pectinata</i> Ehr.	1.2	P
13 <i>S. oblonga</i> Ehr.	0.1	P
14 <i>Asplanchna priodonta</i> Gosse	0.3	P
15 <i>Conochilus unicornis</i> (Rousselet)	8.7	P
16 <i>Filinia longiseta</i> (Ehr.)	r	P
17 <i>Collotheca mutabilis</i> (Hudson)	2.9	P
Copepoda		
18 <i>Acanthodiaptomus denticornis</i> (Wierz.)	r	P
19 <i>Arctodiaptomus laticeps</i> (Sars)	2.4	P
20 <i>Heterocope appendiculata</i> Sars	r	PL
21 <i>Heterocope saliens</i> (Lillj.)	r	PL
22 <i>Macrocyclus albidus</i> Jur.	r	L
23 <i>Cyclops scutifer</i> Sars	74.3	P
24 <i>Megacyclus gigas</i> (Claus)	r	L
25 <i>M. viridis</i> (Jur)	r	L
26 <i>Acanthocyclops vernalis</i> Fischer	r	L
Cladocera		
27 <i>Sida crystallina</i> (O.F.M.)	r	L
28 <i>Holopedium gibberum</i> Zaddach	2.2	P
29 <i>Daphnia longispina</i> (O.F.M.)	4.5	P
30 <i>Bosmina longispina</i> Leydig	16.2	PL
31 <i>Alona affinis</i> (Leydig)	r	L
32 <i>Alonella nana</i> (Baird)	r	L
33 <i>Alonopsis elongata</i> Sars	r	L
34 <i>Chydorus sphaericus</i> (O.F.M.)	r	L
35 <i>Rhyncotalona falcata</i> (Sars)	r	L
36 <i>Polyphemus pediculus</i> L	0.3	L
37 <i>Bythotrephes longimanus</i> Leydig	0.1	P

laticeps were common. *Bythotrephes longimanus*, *Polyphemus pediculus* and *Heterocope saliens* occurred occasionally in low numbers.

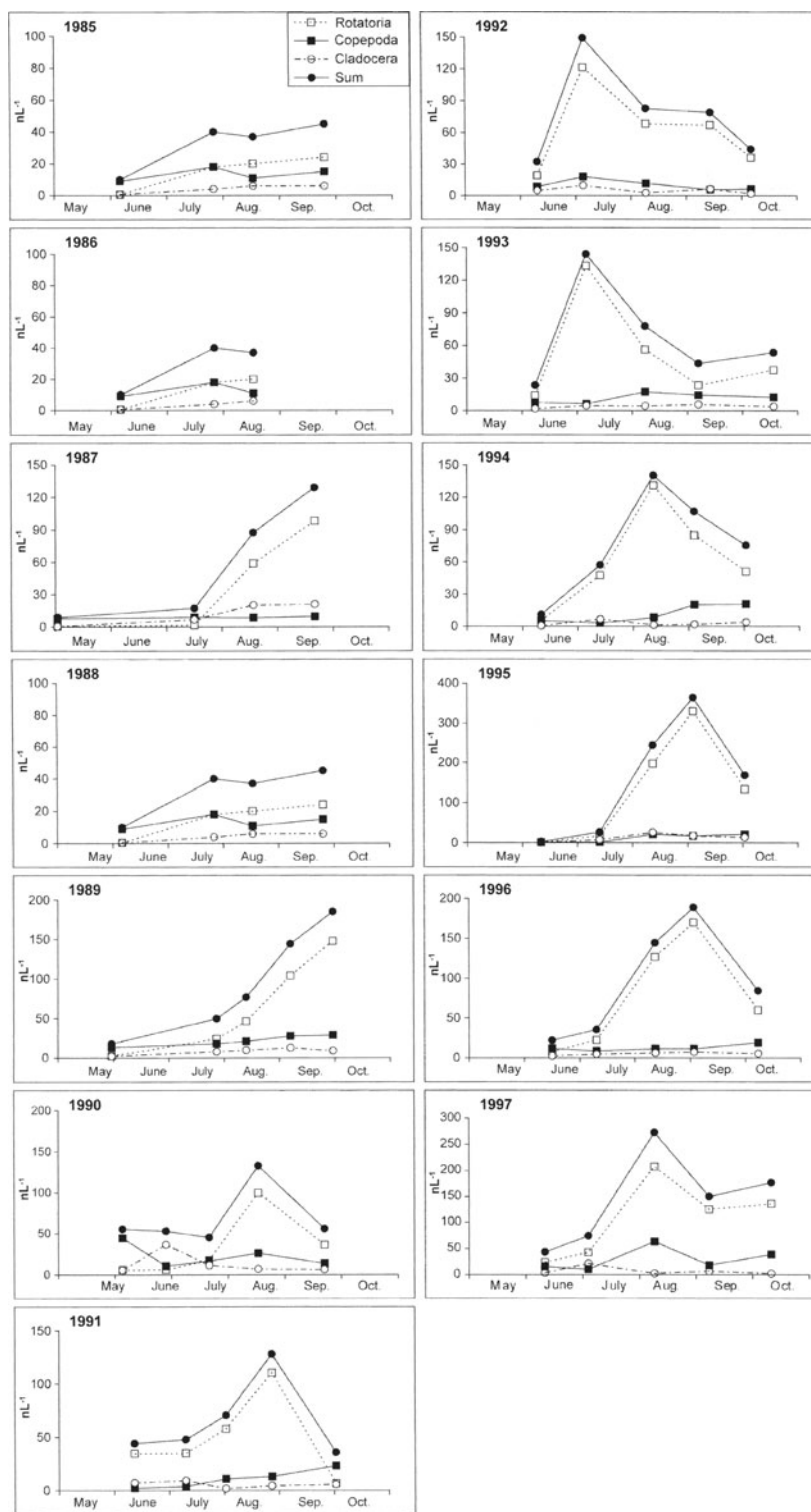


Figure 3. Density (nL⁻¹) of Rotatoria, Copepoda and Cladocera in the plankton community in Lake Atnsjøen during the period 1985–1997. Note different scales.

Seasonal development

The density was low in spring. Most of the species pass the winter as resting eggs, and the new generation start development at the time of ice break-up. *C. scutifer* is the only crustacean species that actively pass the winter in the water, and the differences in density between October and the next spring reflects the mortality during winter (Fig. 2). The mortality was highest during the winter 1990/91 and 1994/1995 when only 12%, respectively 6% of the population survived. During the winters 1989/1990 and 1992/1993 more than 60% of the population survived.

The yearly maximum density in the zooplankton was normally about 140–150 ind. l^{-1} (Fig. 3). The density was, however, extremely low in 1985 and 1988, not exceeding 50 ind. l^{-1} . Highest density was found in 1995, with two to three times the density of the previous years. It was also quite high in the subsequent years, 1996 and 1997.

The plankton community was numerically dominated by rotifers, which sometimes constituted 10–15 times the density of crustaceans (Fig. 3). This is especially accentuated during the zooplankton maxima. The copepods normally constituted 20–30% of the individuals while the cladocerans constituted 10–15%. In spring the proportion of rotifers has increased from less than 15% of the individuals in 1985 to 1990 to between 30% and 80% the last years.

The annual density variations were mainly driven by the density of rotifers. Especially *Kellicottia longispina* varied much during spring, which may reflect that this species is able to survive the winter actively in the plankton. The density of cladocerans and copepods have, however, also varied substantially.

As a mean for the years 1989–1997 the rotifers constituted 81%, the copepods 15% and the cladocerans 4% of the total number of individuals.

By biomass the community was dominated by cladocerans which constituted about 60% of the biomass (Fig. 4). The share of copepods was about 30%, while the rotifers constituted less than 10% of the biomass. The highest share of copepods occurred during early spring. The maximum biomass of rotifers have varied between 7 and 8 $\mu g dw l^{-1}$ most of the years, but in 1995 it increased to nearly 30 $\mu g dw l^{-1}$. It was still higher in 1996 and 1997, with maxima above 10 $\mu g dw l^{-1}$. The maximum biomass of crustaceans have been quite constant, varying around 150 $\mu g dw l^{-1}$. The lowest biomass was found in 1991 and 1994, with less than 100 $\mu g dw l^{-1}$, whereas it was

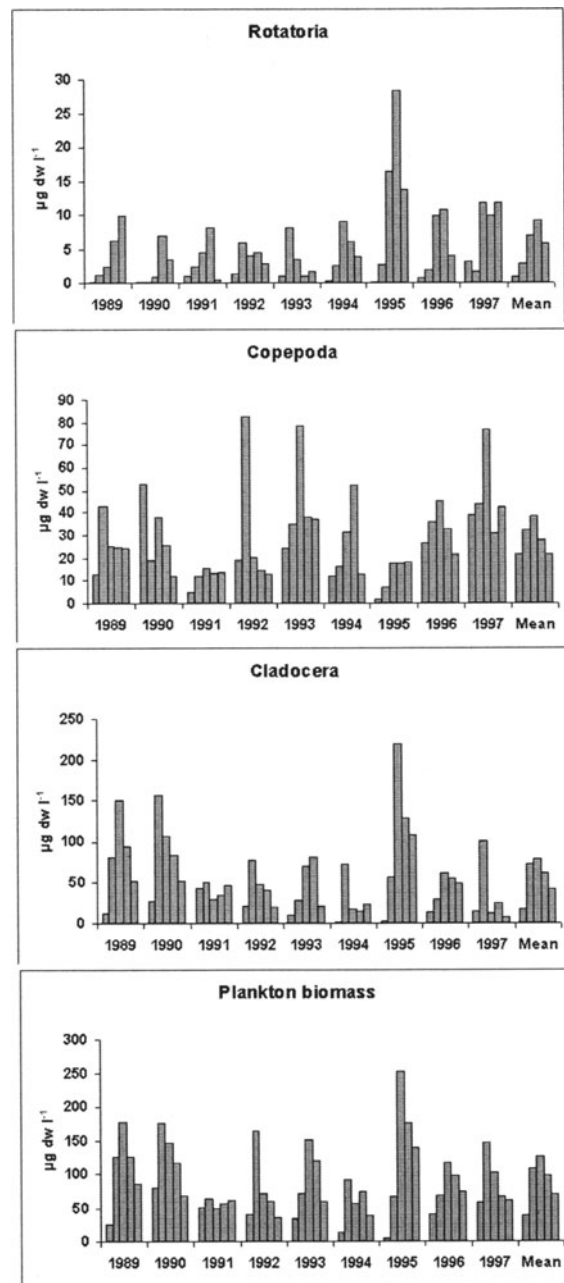


Figure 4. Biomass ($\mu g dw l^{-1}$) of Rotatoria, Copepoda and Cladocera, and the three groups combined, in Lake Atnsjøen during the period 1989–1997, with 5 sampling series per year.

highest in 1995, nearly $240 \mu\text{g dw l}^{-1}$. Normally the total biomass is low in June, less than $50 \mu\text{g dw l}^{-1}$, while it is highest in July, August or September.

Rotifers (Rotatoria)

The rotifers are dominated by three species, *Polyarthra vulgaris* (= *P. dolichoptera* in Dervo, 1988), *Kellicottia longispina*, and *Conochilus unicornis* (= *Ascomorpha* sp. in Dervo, 1988, 1989) (Fig. 5), all with densities above $20\text{--}30 \text{ ind. l}^{-1}$ during their maxima. *P. vulgaris* do have the highest density, usually $80\text{--}90 \text{ ind. l}^{-1}$, and dominate during all maxima except in 1985 when *C. unicornis* made up about 50%. *Keratella cochlearis*, *Keratella hiemalis*, *Asplanchna priodonta* and *Collotheca mutabilis* occur in low numbers, with maxima below 20 ind. l^{-1} .

The time of maximum density have varied between years, occurring both in the beginning of July (in 1992, 1993 and possibly 1986), in August and the beginning of September (1990, 1991, 1994, 1995, 1996 and 1997), and in late September (1987 and 1989) (Figs 2 and 5). A possible fourth type of variation was found in 1985 and 1988 when the density was very low throughout the summer.

The biomass of rotifers are dominated by *P. vulgaris*, with maxima usually between 6 and $8 \mu\text{g dw l}^{-1}$ (Fig. 6). In 1995 the maximum biomass was, however, doubled to about $16 \mu\text{g dw l}^{-1}$. The second most common rotifer, *C. unicornis*, have density maxima normally below $1 \mu\text{g dw l}^{-1}$, but in 1989 it was as high as $2.8 \mu\text{g dw l}^{-1}$. The third most common species, *K. longispina*, have high density in numbers but the biomass is constantly low, with maxima between 0.2 and $0.3 \mu\text{g dw l}^{-1}$. Reflecting the differences in individual body size, the large *A. priodonta* occur in very low densities, but with a biomass similar to *K. longispina*. *A. priodonta* may be very rare in some years. The combined biomass of the other species have gradually increased since 1989, from maxima less than $0.5 \mu\text{g dw l}^{-1}$ to maxima higher than $4 \mu\text{g dw l}^{-1}$. In 1995 the biomass increased 2–3 times or more in the majority of the species. In some species, for example *P. vulgaris*, the biomass was reduced to normal levels in 1996 and 1997 while the biomass of other species remained high until 1997.

Crustaceans

The crustacean fauna was until 1993 numerically dominated by *C. scutifer* and *B. longispina*. *D. longispina* and *H. gibberum* were also important (Fig. 7). The

other species constituted only small fractions of the community. The density of *A. laticeps* was low until 1991, when the population gradually started to increase, and in 1994 it constituted about 40% of the crustacean community in the beginning of June. The general density of crustaceans was, however, very low in June. In 1995 the share of *A. laticeps* was quite low, while it increased again in 1996 and 1997.

C. scutifer dominated the zooplankton community during the ice free period. It was most important in spring when the overall density of crustaceans was low, and in autumn when the new generation of nauplii was present. The relative abundance of *C. scutifer* was lowest in July before the new generation of nauplii appeared.

B. longispina dominated the zooplankton from 1985 to 1991. Later its relative abundance has varied, being particularly low in 1994. The dominance of this species was most pronounced during autumn in 1985, 1986, 1987 and 1988, and in early summer in 1990, 1991 and 1995.

D. longispina occurred in low numbers, and usually constituted only a small fraction of the crustacean community. However, its relative abundance does vary, and in some years, e.g. 1990, 1991, 1992 and 1995, it constituted a substantial proportion of the crustacean community. In September 1992 *D. longispina* constituted nearly 30% of the number of crustaceans.

H. gibberum was a typical summer species, being most common in June and July. It disappeared quite early in autumn and survived the winter as resting eggs. In October only occasional individuals were found.

The yearly biomass maxima of crustaceans have varied between $62 \mu\text{g dw l}^{-1}$ in 1991 and $235 \mu\text{g dw l}^{-1}$ in 1995 (Fig. 8). The common maximum level seems to be between 150 and $200 \mu\text{g dw l}^{-1}$, which correspond to $0.5\text{--}0.7 \text{ g dw m}^{-2}$. The contribution by each species to the total biomass varies from year to year. *B. longispina* has the highest biomass, with maximum about $150\text{--}200 \mu\text{g dw l}^{-1}$. The biomass of the other species never exceeded $60\text{--}70 \mu\text{g dw l}^{-1}$.

Diversity

The diversity at the community level, with rotifers and crustaceans combined, is high to very high, with $H > 1.500$ (Table 3). The diversity is, however, low in the crustaceans because of few species. There are no systematic trends in the diversity, and maximum

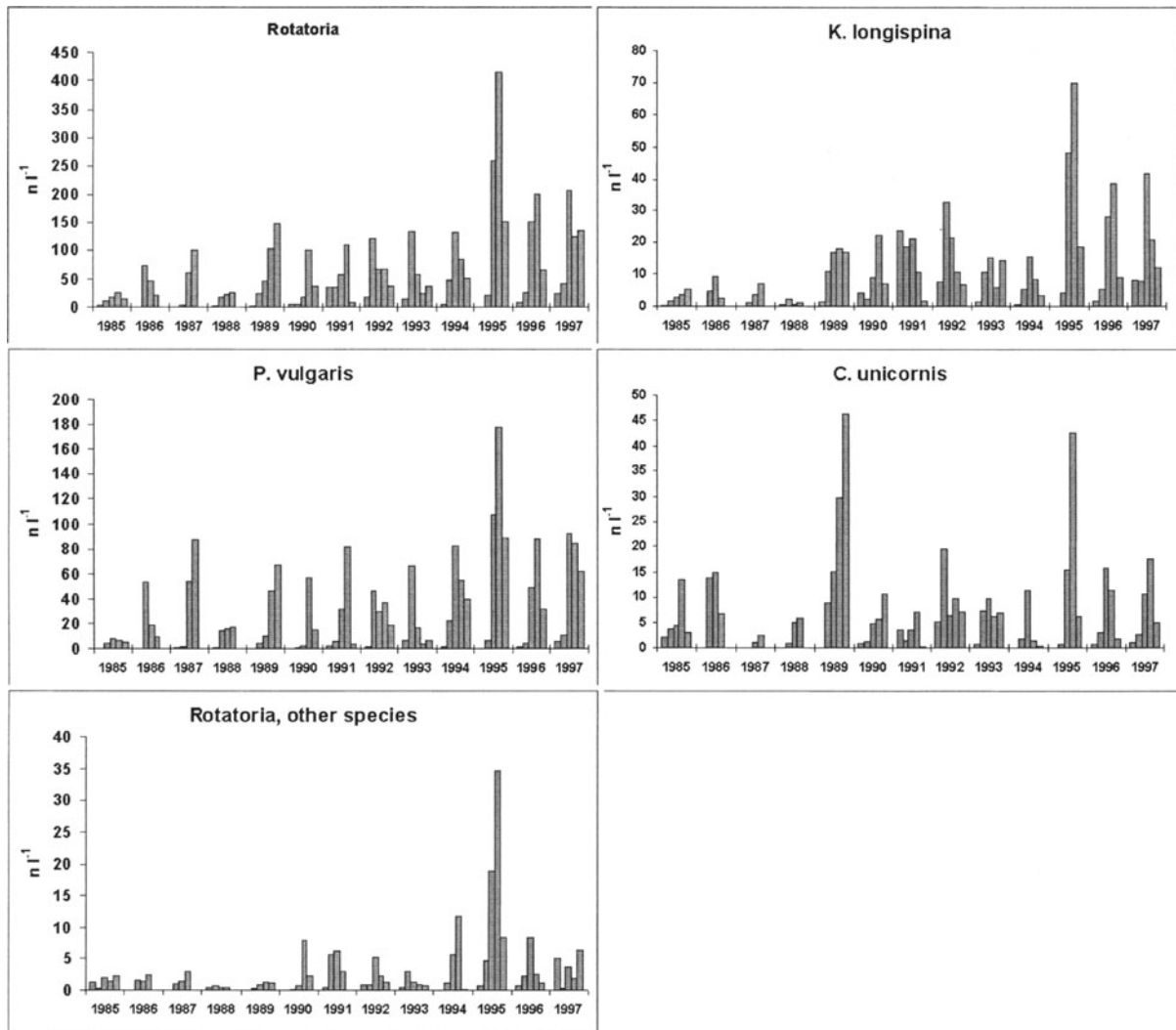


Figure 5. Density ($n\ l^{-1}$) of the dominating species of Rotatoria in Lake Atnsjøen during the period 1985–1997. Note different scales.

diversity may occur in all months. In all the three groups the diversity is generally highest in July and lowest in October, but the differences are small. The variation between years is also quite small with the overall lowest and highest diversity in 1990 and 1996, respectively.

Life cycles

A short summary of the life cycle of the main crustacean species is given below.

Cyclops scutifer

Cyclops scutifer is the only common species of cyclopoid copepods in the plankton. The main structure

in the life cycle of *Cyclops scutifer* is illustrated by the development in 1993 and 1996 (Fig. 9). The population is divided into two fractions in spring, with a small fraction of large nauplii and a large fraction of copepodites (Cop. II–IV). The instars occurring in June reflects the over-wintering population, even if the small number of adults indicates that some development has occurred after the break-up of the ice. In July both nauplii and copepodites have developed further and are found as older copepodites or adults, and a small number of females have already started reproduction. The main reproduction period is August and September. The first nauplii of the new generation may appear as early as in the beginning of July, but high numbers are not found until the beginning of August.

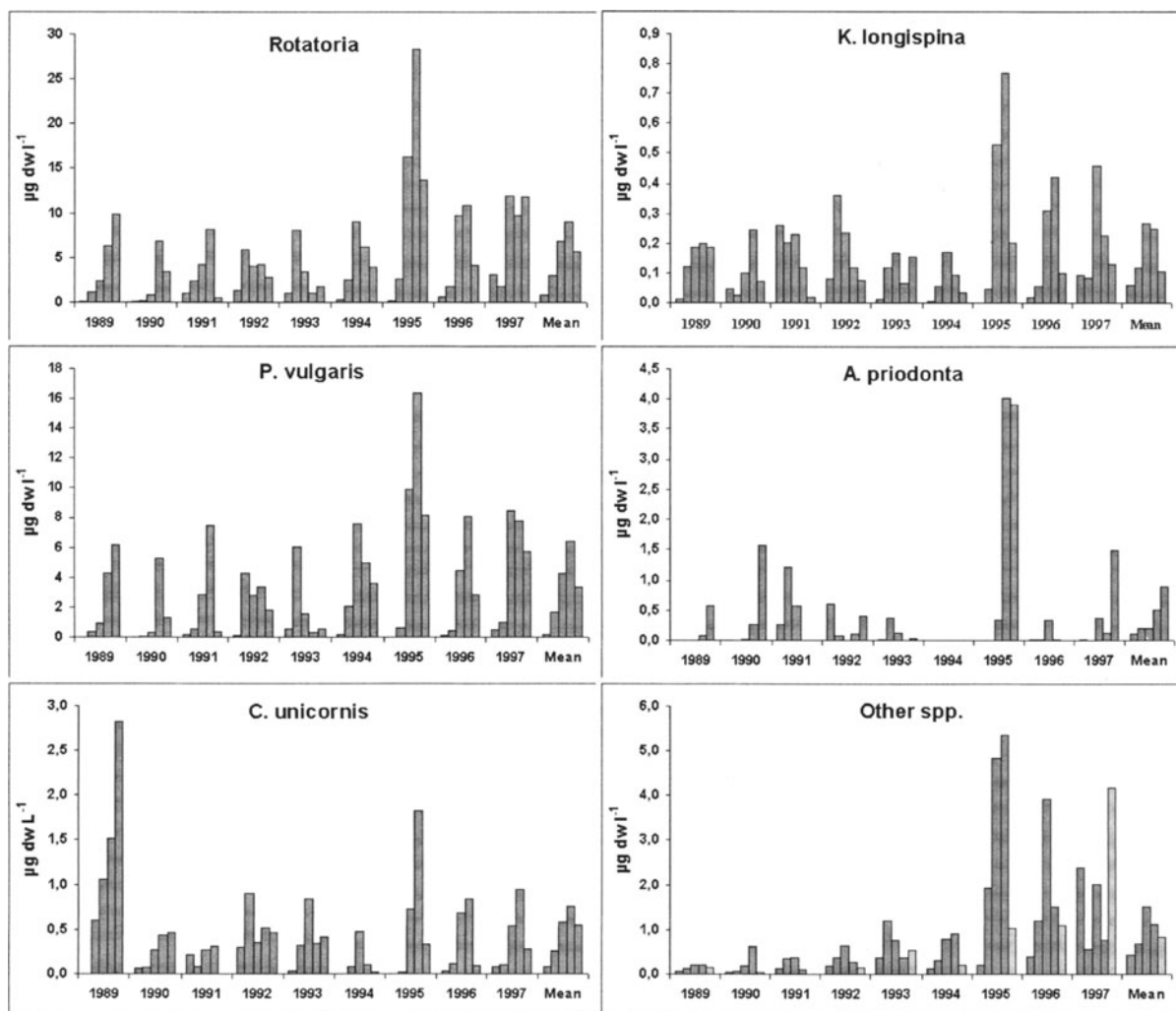


Figure 6. Biomass ($\mu\text{g dw l}^{-1}$) of Rotatoria, and the main species Lake Atnsjøen during the period 1989–1997, with 5 sampling series per year. Note different scales.

In October the population normally consists of large numbers of nauplii, a few large copepodites and even fewer adults. The adults disappear before the onset of winter.

The main part of the population reproduce after one year, while a small fraction has a two year cycle. The two-year fraction consists of individuals that pass the first winter as small nauplii, and are found as Cop. II–V in October the following autumn. The main part of the population pass the winter as large nauplii and small copepodites.

This life cycle pattern was observed in most years. However, in 1989 and 1990 the pattern differed substantially (Fig. 9). In these years the population was clearly divided into three fractions in the beginning

of June: nauplii, small copepodites, and large copepodites. These three fractions were still traced later in summer. In these years there was a larger fraction with a two year life cycle.

Bosmina longispina

Bosmina longispina is the dominating cladoceran (Fig. 10). In all investigated years, the population was dominated by females without eggs (F), whereas females with eggs (F_{ov}) were found in low numbers. There was no clear correlation between number of females with eggs, eggs per female and increase or decrease in population density. Juveniles occurred only in large numbers in early summer. Males were recorded from August with maxima of more than 10% of

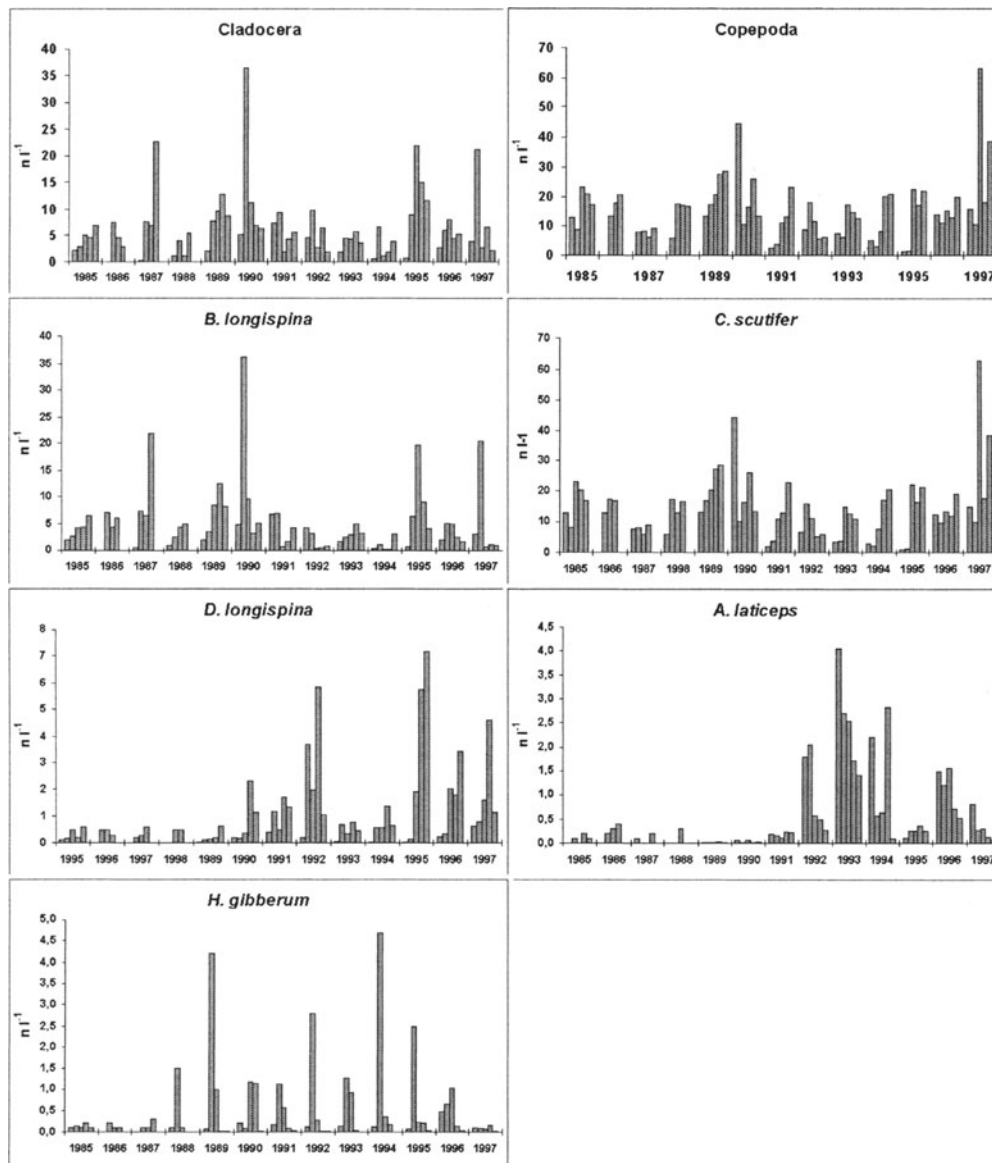


Figure 7. Density ($n\ l^{-1}$) of the dominating species of Crustacea in Lake Atnsjøen during the period 1985–1997. Note different scales.

the population in September. The first production of resting eggs occurred in August, and from September most of the eggs were resting eggs.

Daphnia longispina

Daphnia longispina occurred in low densities, but still constituted a significant part of crustacean biomass. With the exception of 1989 and 1995, the species demonstrated a development with a small maximum in the beginning of July, and a somewhat larger maximum in the beginning of September (Fig. 11). The

major part of the population survives the winter as resting eggs, and density was at its lowest in beginning of June.

The population was dominated by females without eggs (F). Juveniles have the highest densities in July when the first total maximum was observed. Later the density of juveniles was very low. Females with eggs (F_{ov}) occurred in low densities throughout the summer, but increased during autumn. In 1992, however, the number of females with eggs reached its maximum in the beginning of July, during the first maximum.

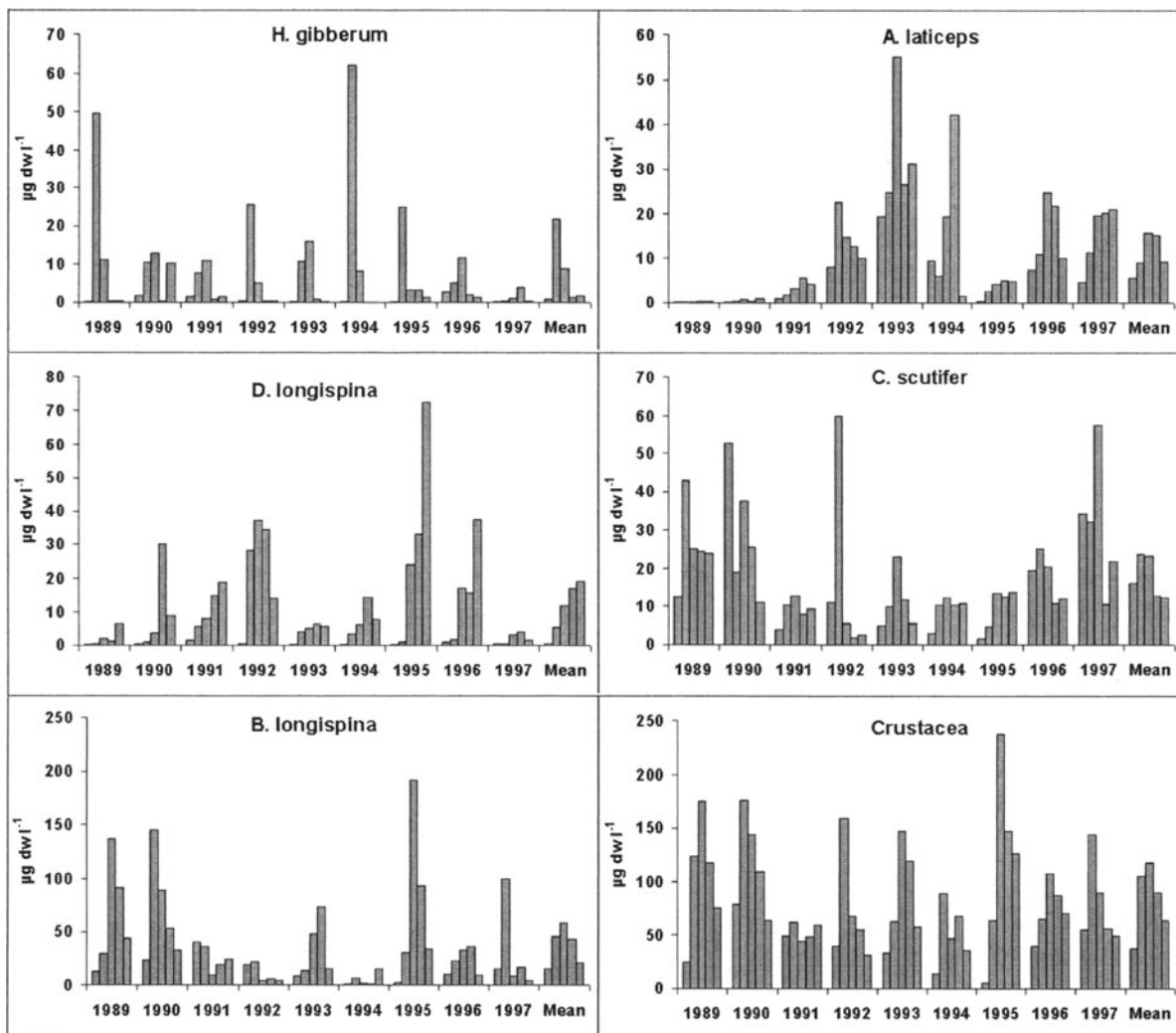


Figure 8. Biomass ($\mu\text{g dw l}^{-1}$) of total Crustacea, and the main species, in Lake Atnsjøen during the period 1989–1997, with 5 sampling series per year. Note different scales.

There was no clear correlation between the density of females with eggs and the development in population density. Males occurred in small densities in late autumn.

Holopedium gibberum

H. gibberum occurred in low numbers, usually not exceeding 2–3 ind. l^{-1} (Fig. 12). It survives the winter as resting eggs, and in the beginning of June the population was dominated by juveniles. The summer maximum usually occurred in July. The density was very low in August, and in the beginning of October only occasional individuals were found. No

males were observed, and the reproduction seems to be entirely parthenogenetic.

There are two different patterns of yearly development. In 1989, 1992, 1994 and 1995 the population of *H. gibberum* showed a well-defined maximum in July, while no well-defined maximum was seen in 1990, 1991 and 1993.

Arctodiaptomus laticeps

Arctodiaptomus laticeps usually occurred in low numbers (Fig. 13). It passes the winter as resting eggs, and occur in very low numbers in early summer. Maximum density may occur from July (1990, 1992) to September (1995). The density structure indicates a

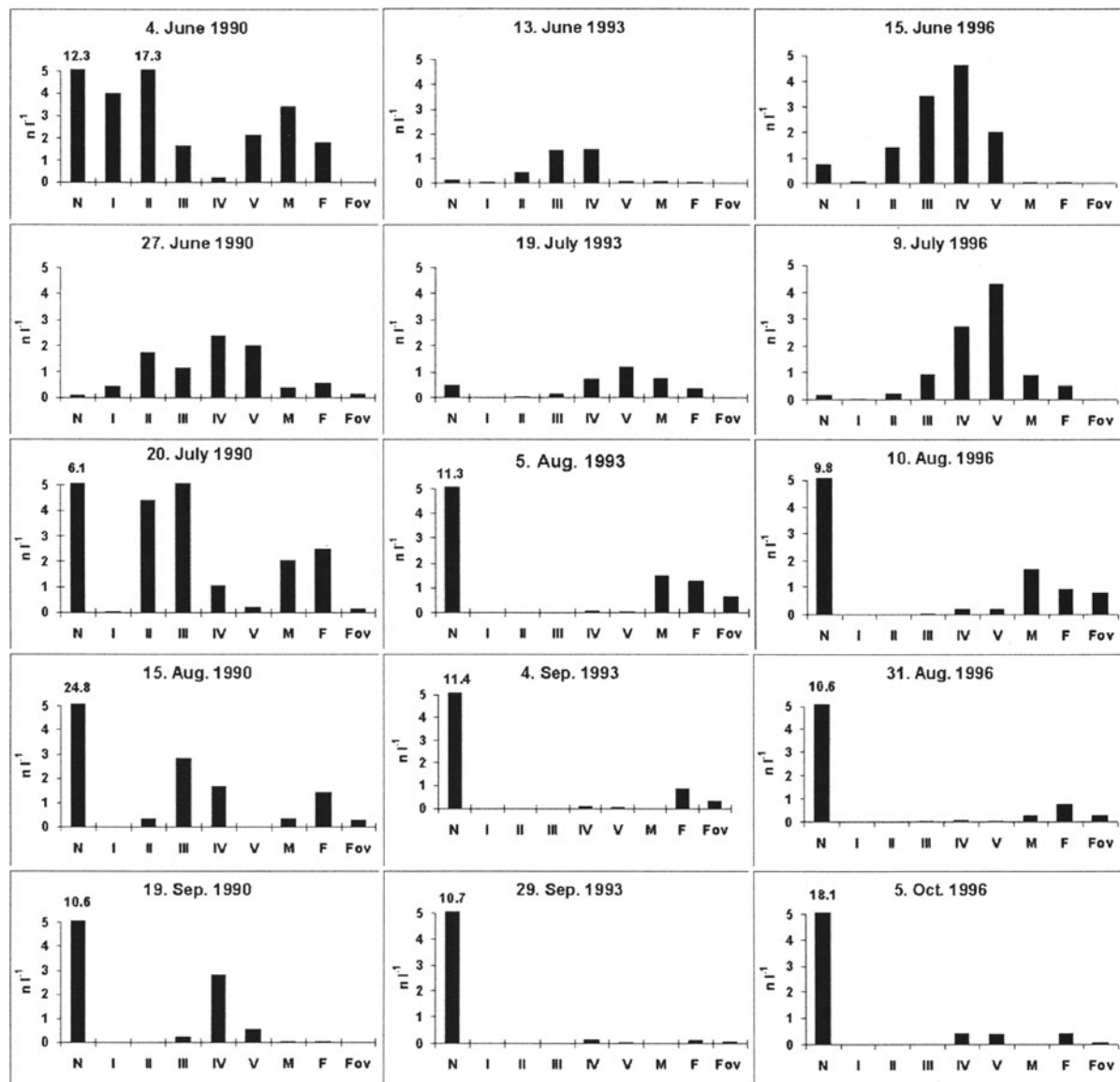


Figure 9. The occurrence ($n\ l^{-1}$) of the different developmental stages in *Cyclops scutifer* in Lake Atnsjøen in 1990, 1993 and 1996. N = nauplii, I–V = copepodites I–V, M = males, F = females without eggs, F_{ov} = females with eggs.

second generation during autumn. The first generation reproduced in July, mainly producing resting eggs, but a small fraction produced subitane eggs. The second generation reproduced in September/October, only producing resting eggs.

Vertical distribution and migration

The plankton community has a marked vertical distribution with maximum density usually between 5 and 10 m during day (Fig. 14). The density was normally

low near the surface and in the hypolimnion. The depth of maximum density increased during summer, following the downward movement of the thermocline and the increasing transparency. In late September and early October the temperature stratification broke down, and during the autumn circulation the vertical distribution become less pronounced.

The rotifers stay somewhat closer to the surface than the crustaceans (Fig. 14), and the copepods somewhat deeper than the cladocerans. The differences were, however, usually small.

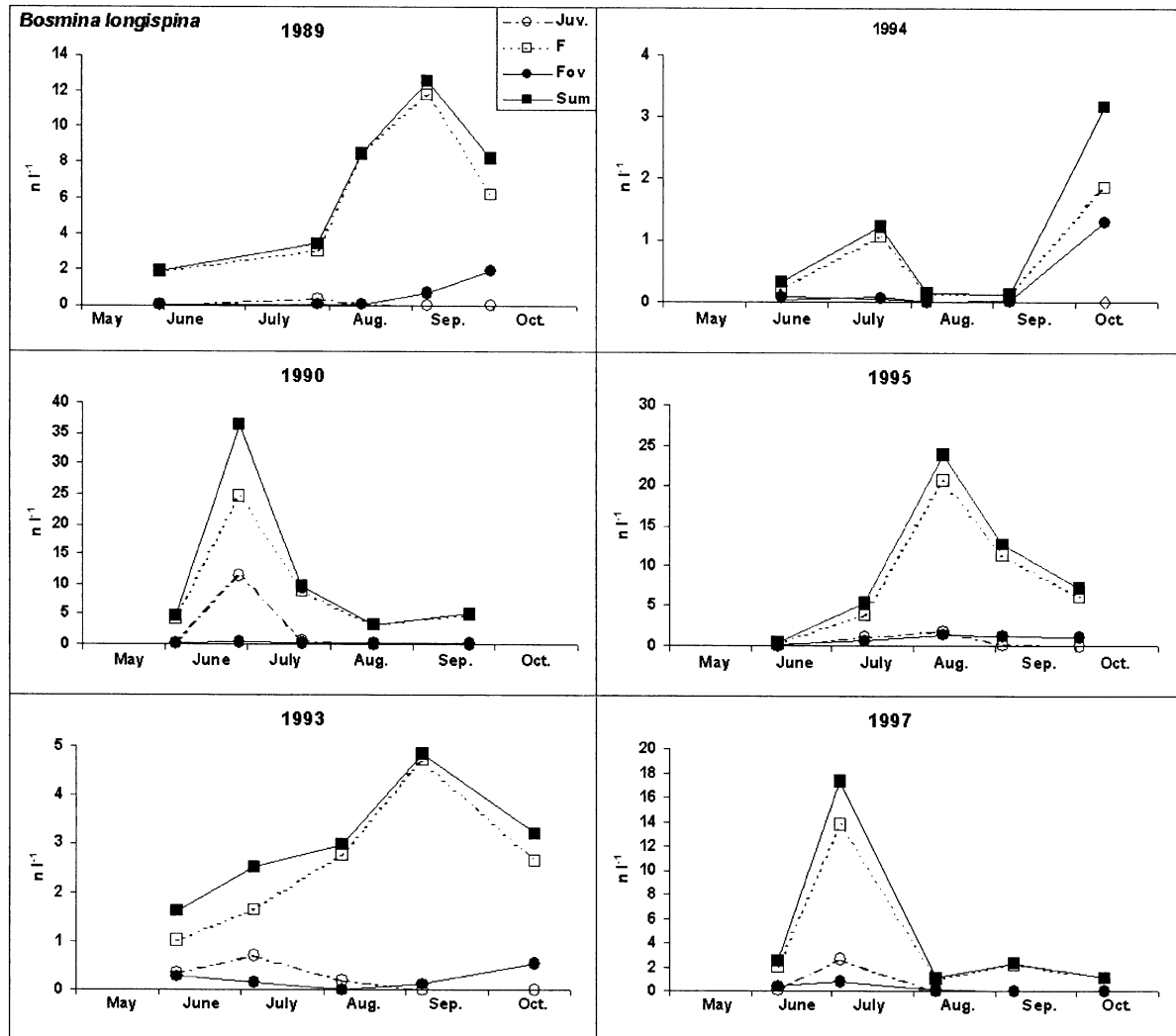


Figure 10. Density ($n\ l^{-1}$) of *Bosmina longispina* juveniles (Juv.), and adult females with (Fov) and without eggs (F) in Lake Atnsjøen in selected years. Note different scales.

The diurnal vertical migration was quite small in the rotifers, small or absent in the copepods, and quite pronounced among the cladocerans, especially in *B. longispina* (Fig. 15). During night maximum density was found close to surface.

Horizontal distribution

The first years the material was sampled from several stations both along and across the lake. There were sometimes great differences between the different stations, but there seem to be no systematic pattern. There are, however, a tendency of increasing density towards the outlet, and decreasing density towards the northern

shore across the lake, with highest density at station D1 and lowest at B1.

DCA and PCA ordination

Our analysis show no strong correlation between environmental factors and the community structure and variation, except for the marked effects of the large flood in 1995 when the density increased threefold and the biomass twofold because of increased input of allochthonous material. The only other factor of significant importance is water temperature, controlling the first axis in the DCA plot ($r^2 = 0.55$). All the other parameters have low to very low r^2 . There is no correlation with the input of allochthonous mater-

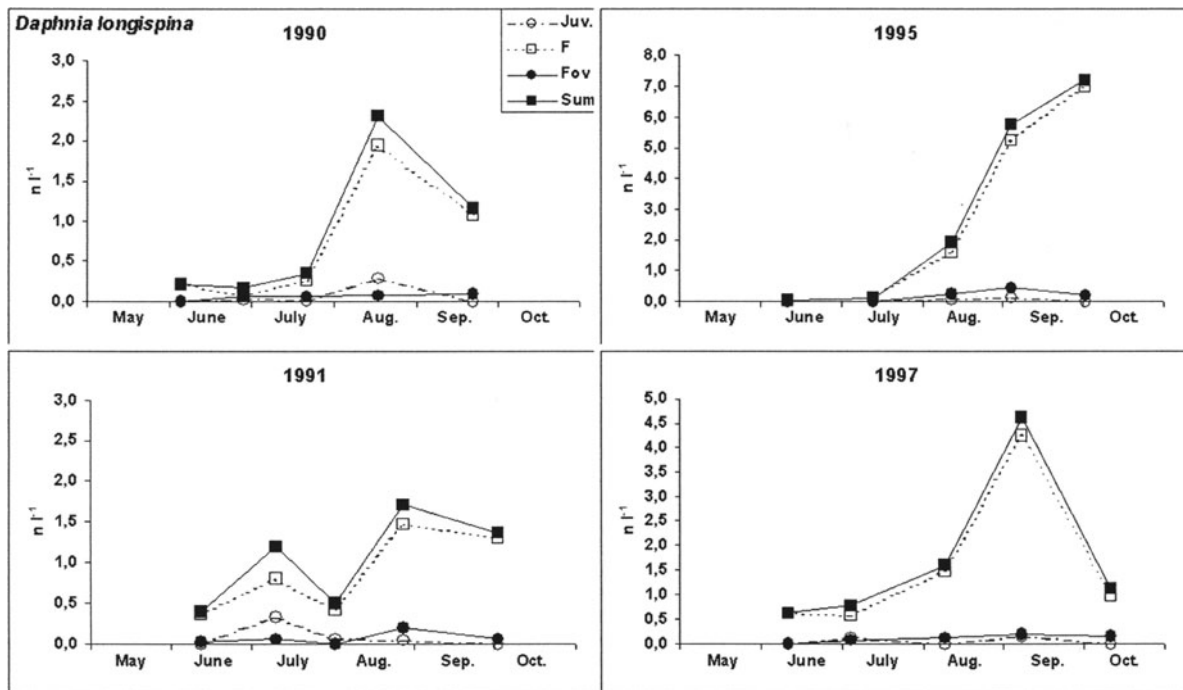


Figure 11. Density ($n\ l^{-1}$) of *Daphnia longispina* juveniles (Juv.), and adult females with (F_{ov}) and without eggs (F) in Lake Atnsjøen in selected years. Note different scales.

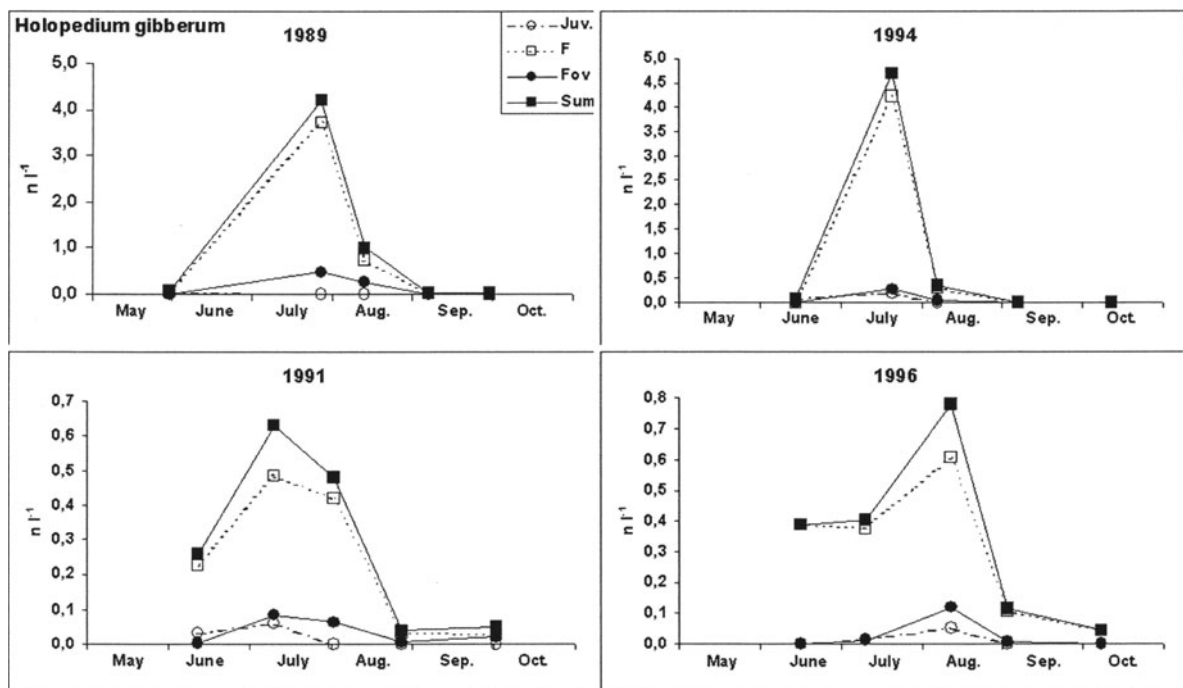


Figure 12. Density ($n\ l^{-1}$) of *Holopedium gibberum* in Lake Atnsjøen in selected years. Note different scales.

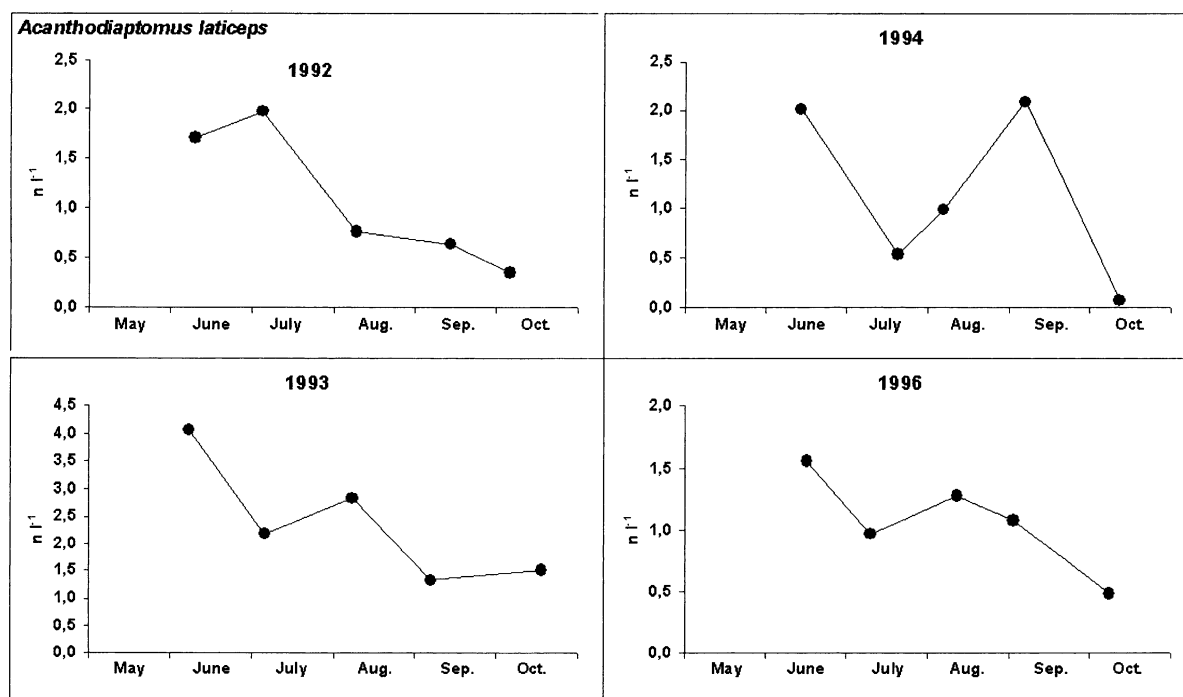


Figure 13. Density (n l⁻¹) of *Arctodiatomus laticeps* in Lake Atnsjøen in selected years. Note different scales.

ial. It is also interesting to observe that the number of day degrees above 4 and 7 °C, respectively, is of small importance. Other climatic factors, and also the length of the ice free period, appear to be of no importance. Which factors that reflects the second axis are even more diffuse, and no factor is significant.

In the PCA analysis the first axis is highly correlated with the number of individuals ($r^2 = 0.78$), while the second most important factor is water temperature ($r^2 = 0.43$). No factors are significantly correlated to the second axis.

Discussion

Of the 37 species observed in the plankton, 24 are planktonic or plankton-littoral, while the remainder are typical littoral and/or bottom-living species occurring only occasionally in the plankton. The plankton community in Lake Atnsjøen is dominated by cold-stenothermic and eurythermic species, and is typical for oligotrophic and cold lakes (Flössner, 1972, 2000; Blakar & Jacobsen, 1979; Aagaard & Dolmen, 1996). The species composition have varied little during the study period.

All the observed species of crustaceans are common in southern Norway (Aagaard & Dolmen, 1996). The zoogeographical distribution of rotifers in Norway is poorly known, but all the observed species, maybe except of *Synchaeta oblonga*, which is new to Norway, are believed to be common in southern Norway (Aagaard & Dolmen, 1996).

The number of zooplankton species found in Lake Atnsjøen is similar to what is found in comparable Norwegian lakes (Halvorsen, 1981), and is also similar to cold oligotrophic lakes in other areas (Patalas, 1971). Among the crustaceans, two dominating species of copepods and three species of cladocerans are common over large areas (Patalas, 1971; Halvorsen, 1981). The zooplankton community in Lake Atnsjøen is, with some exceptions, similar to that in Lake Øvre Heimdalsvatn, a subalpine lake (1090 m a.s.l) strongly influenced by high through-flow (Larsson, 1978). Here the community is dominated by the same three species of rotifers (*Polyarthra vulgaris*, *Kellicottia longispina*, and *Conochilus unicornis*), the same species of cladocerans (*Holopedium gibberum*, *Bosmina longispina* and *Daphnia longispina*) and by *C. scutifer*. *A. laticeps* was not found in that lake, whereas *Heterocope saliens* was the only calanoid copepod. A similar number of dominant species also

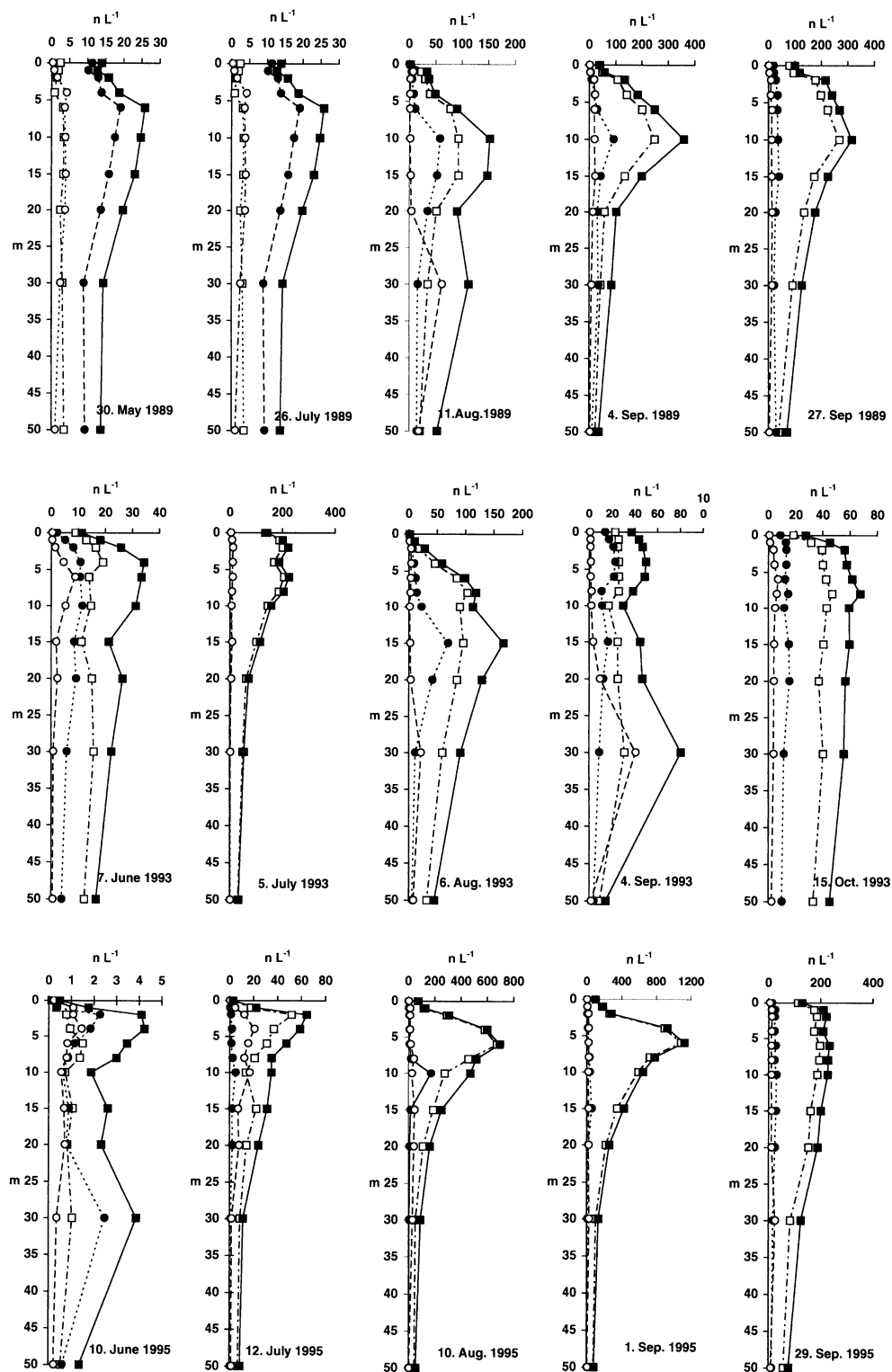


Figure 14. The vertical distribution of Rotatoria (\square), Copepoda (\bullet), Cladocera (\circ) and the three groups combined (\blacksquare) in Lake Atnsjøen in 1989, 1993 and 1995. Day samples.

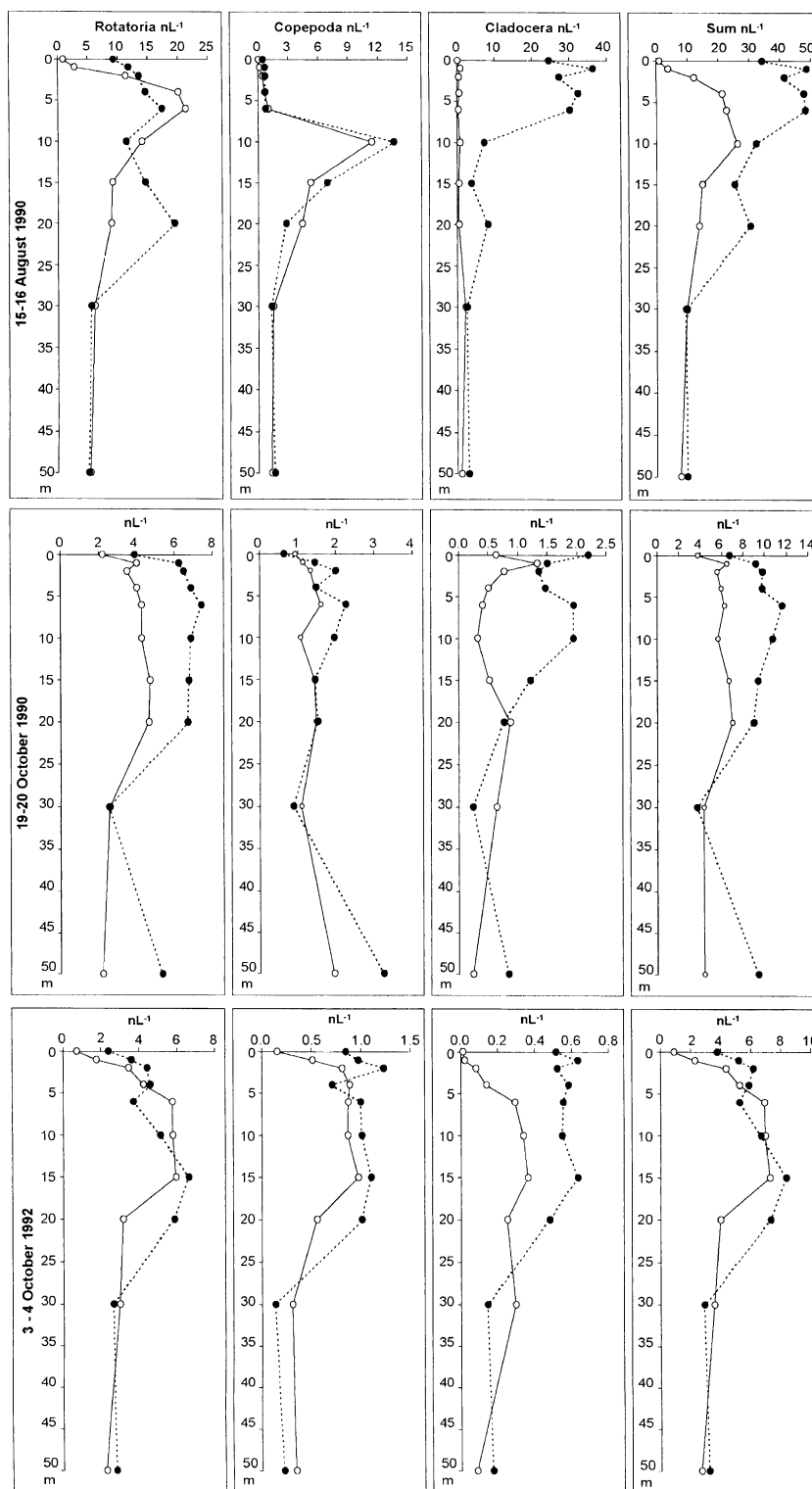


Figure 15. The vertical distribution of Rotatoria, Copepoda and Cladocera in Lake Atnsjøen day (○) and night (●), 15–16 August, and 19–20 September, 1990, and 3–4 October, 1992.

Table 3. Shannon–Wiener's diversity-index in the zooplankton community in Lake Atnsjøen in the period 1989–1997.

Community	June	July	Aug.	Sep.	Oct.	Mean
1989	0.987	1.752	1.764	1.636	1.526	1.533
1990	0.811	1.126	1.687	1.660	1.784	1.414
1991	1.484	1.916	1.681	1.254	1.323	1.531
1992	1.989	1.781	1.793	1.634	1.733	1.786
1993	1.916	1.437	1.503	2.004	1.991	1.770
1994	1.906	1.686	1.372	1.556	1.255	1.555
1995	1.721	1.903	1.711	1.684	1.657	1.735
1996	1.817	2.083	1.918	1.655	1.774	1.849
1997	2.031	1.884	1.671	1.578	1.609	1.755
Mean	1.629	1.730	1.678	1.629	1.628	1.659

Rotatoria	June	July	Aug.	Sep.	Oct.	Mean
1989	1.017	1.287	1.339	1.190	1.102	1.187
1990	1.113	1.398	1.442	1.191	1.342	1.297
1991	0.964	1.442	1.321	0.785	1.209	1.144
1992	1.474	1.272	1.407	1.216	1.329	1.340
1993	1.332	1.123	1.094	1.611	1.582	1.348
1994	1.411	1.179	1.131	1.142	0.655	1.104
1995	1.172	1.363	1.298	1.405	1.190	1.286
1996	1.644	1.646	1.594	1.351	1.329	1.513
1997	1.671	1.547	1.377	1.181	1.309	1.417
Mean	1.311	1.362	1.334	1.230	1.227	1.293

Crustacea	June	July	Aug.	Sep.	Oct.	Mean
1989	0.464	0.844	0.759	0.624	0.631	0.664
1990	0.357	0.604	0.819	0.727	0.756	0.653
1991	0.862	1.105	0.632	0.795	0.739	0.826
1992	1.082	1.228	0.814	1.088	0.950	1.032
1993	1.114	1.470	1.077	1.015	0.911	1.117
1994	0.989	1.411	0.734	0.699	0.566	0.880
1995	1.058	1.061	0.882	1.041	0.996	1.008
1996	0.905	1.048	1.186	1.141	0.788	1.013
1997	0.846	0.781	0.306	0.690	0.270	0.578
Mean	0.853	1.061	0.801	0.869	0.734	0.864

occurred in the arctic lake Thingvallavatn in Iceland (Antonsson, 1992). A even lower number of species was found in the glacier fed mountain lake Gjende (984 m a.s.l.), and the middle alpine lake Bessvatn (1374 m a.s.l.) (Elgmork & Eie, 1989).

During the period 1985–1997, community structure, seasonal development, vertical distribution, and density, have changed much between years. There

was, however, only a small variation in the occurrence of species. These yearly variations are surely connected directly or indirectly to variations in temperature, availability of food, predation, inter- and intraspecific competition and water-flow (renewal time), but it is difficult to detect these correlations as the different factors are strongly interconnected, and they probably also mask each other.

The density of rotifers and crustaceans have varied throughout the study, with lowest densities in 1985 and 1988, about 50 ind. l⁻¹, and highest in 1995, nearly 450 ind. l⁻¹. Normally the maximum density has been just below 150 ind. l⁻¹. The two years with the lowest densities, 1985 and 1988, had high precipitation and constant high through-flow during the summer. The high density in 1995 was caused by high input of allochthonous material and low through-flow during summer and autumn, although the spring flood was very high. In most of the species the biomass increased 2–3 times or more. The density was still high in 1996 and 1997, which may be a long-term effect of the flood in 1995. It may also reflect that these two years were the driest years during the study period, resulting in a low through-flow.

The density of rotifers is comparable with that in Lake Øvre Heimdalsvatn (Larsson 1978), and in Lake Thingvallavatn (Antonsson 1992). The most numerous rotifer in Lake Atnsjøen was *P. vulgaris*, while *C. unicornis* was the most common species in Lake Øvre Heimdalsvatn. *K. longispina* was the second most common species in both lakes. Similar species do also dominated in Lake Thingvallavatn (Antonsson 1992).

The density of crustaceans, however, was higher in Lake Atnsjøen than in Lake Øvre Heimdalsvatn, which can be explained by the much higher through-flow in Lake Øvre Heimdalsvatn (Larsson, 1978). This is in accordance with Shiel & Walker (1984), who found that lakes with retention time of 6 month or shorter are dominated by rotifers, with a small fraction of copepods, while lakes with retention time longer than 12 months are dominated by crustaceans. Summer forms of rotifers also dominate in lakes with long retention time (Shiel & Walker, 1984). The density of crustacean in Lake Atnsjøen was higher than in the delta area of the lowland Lake Randsfjorden, which was also affected by high through-flow (Halvorsen et al., 1996). The density was much higher in Atnsjøen than in the more alpine lakes Gjende and Bessvatn (Elgmork & Eie, 1989).

Compared with other large Norwegian lakes, the zooplankton biomass in Lake Atnsjøen is low (Kjellberg, 1999), with a summer mean of about $0.2\text{--}0.4\text{ g m}^{-2}$. It is also somewhat lower than in Lake Øvre Heimdalsvatn (Larsson, 1978), which is a much more shallow lake, and it is much lower than in Thingvallavatn (Antonsson, 1992).

Water temperature strongly influences the physical, chemical and biological processes in lakes, and is thus a key factor in understanding the lifecycle of species, and the variations in the plankton community (Bottrell et al., 1976; Moore, 1977; Wetzel, 2001). The DCA and PCA analyses shows some correlation between the community structure and lifecycle of the dominant species in Lake Atnsjøen and water temperature. We did not, however, find any correlation with other climatic factors such as number of degree days higher than 4 and 7 °C.

The phytoplankton community is dominated by small species (μ -algae, $<20\text{ }\mu\text{m}$), together with small Chrysophyceae and Cryptophyceae (Dervo, 1988; Fagernæs, 1989; Brettum & Halvorsen, 2004). These small algae favour the sedimentators among the rotifers, such as *P. vulgaris* and *C. unicornis*, and the microfiltrators, such as *H. gibberum*, *B. longispina*, *D. longispina* and *A. laticeps*. *B. longispina* utilise algae of different size ($1\text{--}20\text{ }\mu\text{m}$) (DeMott, 1982; Hessen, 1985) and is both a micro- (Gliwicz, 1969) and macrofiltrator (Geller & Müller, 1981; Persson, 1985). Consequently, nearly all the phytoplankton species and biomass are available as food for this species.

The zooplankton in Lake Atnsjøen is to a great extent dependent on allochthonous material as a food resource, as the production of phytoplankton probably does not sustain the production of zooplankton (Dervo, 1988). The phytoplankton biomass is very low, normally less than $0.40\text{ mm}^3\text{ l}^{-1}$ ($\approx 0.40\text{ mg l}^{-1}$) (Dervo, 1988; Fagernæs, 1989; Brettum & Halvorsen, 2004). The minimum nutritional concentration required for the survival of individual daphnids is estimated at about 0.05 mg C l^{-1} (Lampert, 1977; Kersting, 1983), and even more during reproduction (Lampert, 1978). In Lake Atnsjøen the mean food concentration constituted by algae in the epilimnion is usually lower, but near the surface it may be as high as 0.17 mg C l^{-1} (Dervo, 1988).

The input of allochthonous material to Lake Atnsjøen is not known, but the results from 1995 clearly shows the importance of the allochthonous input (Brabrand, 1998). This year the input of allochthon-

ous material overruled all other environmental factors. A short, but very high water flow, where large floodplains were flooded, occurred at the end of May and beginning of June this year (Tvede, 2004), and a large amount of organic and inorganic material was transported into the lake. The smallest Secchi disk transparency ever measured, 4.3 m, was found in June 1995, and the transparency was reduced throughout the summer. This large input of allochthonous material, together with a parallel increase in production of phytoplankton (Brettum & Halvorsen, 2004), resulted in a pronounced increase in zooplankton abundance and production in 1995. Compared with the years before, the density of zooplankton increased nearly three times, and the biomass was nearly doubled. The increase was most pronounced in rotifers, smaller in cladocerans and smallest in copepods.

The flood in 1995 had a restricted influence on the productivity, and already in 1996 and 1997 the standing biomass was only slightly higher than before the flood. According to Bogen (2004) the fluvial transport upstream the lake was more than tenfold in 1996 and 1997 compared to 1994, as large new areas became exposed to erosion after the flood in 1995. This increase had, however, only a small effect on the zooplankton production in Lake Atnsjøen, indicating that the increased material load was deposited on the floodplains before reaching the lake.

The increase in density of the species is in accordance with what can be expected knowing the nutritional requirements of the species. Especially *B. longispina* is known as a diet generalist (DeMott, 1982; Hessen, 1985). This is also in accordance with what is found in the potamoplankton in large rivers, where the rotifers after high flow increase in population densities much faster than cladocerans, while the copepods responds even slower (Shiel & Walker, 1984). The rotifers are thus strongly dominating in river reservoirs with high through-flow and short retention time (Shiel & Walker, 1984). The same is also partly true in Øvre Heimdalsvatn (Larsson, 1978). Increased input of allochthonous material has a similar effect as eutrophication. Rotifers are known to respond faster to a eutrophication process than the more slow growing crustaceans (Beaver & Crisman, 1990; Lair, 1991).

The input of allochthonous material into Lake Atnsjøen is probably of the same magnitude, or even higher, than in Lake Øvre Heimdalsvatn (Larsson et al., 1978). In this lake, nearly 1/3 of the inflowing allochthonous material was transported out of the

lake again during high water flows. In Lake Atnsjøen a larger proportion of the imported material will be deposited and remain in the lake due to longer retention time.

The relatively high biomass and density of zooplankton in 1989 can not be directly correlated to an increased input of allochthonous material according to the water discharge at the outlet of Lake Atnsjøen (Tvede, 2004). The DCA and PCA analyses showed no significant correlation between transparency (indicating input of allochthonous material), and neither community structure nor biomass. We need more information about the correlation between water-flow, flood-level, and input of allochthonous material to really understand how these factors influence zooplankton production. The nutritional quality of the allochthonous material is probably also of major importance in this connection.

The food condition influence the vertical and horizontal distribution of the zooplankton, and to what extent the species are migrating (Dervo, 1988). In 1985 the correlation between the distribution of phytoplankton and *B. longispina* during night was significant, while the correlation was less pronounced during day (Dervo, 1988). *B. longispina* is the only crustacean with pronounced vertical migration, while both *H. gibberum* and *D. longispina* lack vertical migration some years. This is probably caused by scarcity of suitable food items in the lake, and to obtain enough food to grow and reproduce these species have to stay in the surface water with the best food conditions both during day and night, thus exposed to heavy predation risk. According to Hessen (1988) *B. longispina* have lower nutritional requirement than *H. gibberum* and *D. longispina*. With very low food concentration, as in 1987, even *B. longispina* lacked vertical migration (Dervo, 1988). The restricted abundance of food may explain the yearly variation in the density of some species. The increased occurrence of *D. longispina* and *A. laticeps* the last years can be explained by a combination of increased phytoplankton production, increased input of allochthonous material, and more favourable temperatures (cf. Nordli & Grimenes, 2004).

Fish predation is an important factor regulating both the density, life cycle and spatial distribution of zooplankton (Brooks & Dodson, 1965; Nilsson & Pejler, 1973; Zaret & Kerfoot, 1975; Langeland, 1978). Lake Atnsjøen have relatively large populations of Arctic charr (*Salvelinus alpinus*) and brown trout (*Salmo trutta*). The Arctic charr live almost

exclusively on zooplankton, while the diet of the trout is more variable including also zoobenthos, surface insects, and small fish (Dervo, 1988; Hegge, 1988; Hesthagen et al., 1989; Saksgård & Hesthagen, 2004). The population of Arctic charr is 3–4 times larger than the population of brown trout, and the predation on zooplankton is quite high (Saksgård & Hesthagen, 2004). Especially the larger specimens of cladocerans and copepods such as *D. longispina*, *Bythotrephes longimanus* and *H. appendiculata* are eaten. *B. longispina* is also important, especially specimens larger than 0.8 mm (Dervo, 1988; Hegge, 1988; Saksgård & Hesthagen, 2004). *C. scutifer*, the most common species, is apparently little affected by fish predation due to their behaviour and habitat choice staying in deep waters during both day and night (Dervo 1988). The low densities of *H. saliens*, *D. longispina* and *H. gibberum* are to some extent caused by high predation pressure from fish (Dervo, 1988; Hesthagen et al., 2004; Saksgård & Hesthagen, 2004). The variation between years in population size of *D. longispina* may also reflect reduced predation pressure. *A. laticeps* seems not to be affected by predation. The carnivore species *B. longimanus* occur only in very low density, but is highly selected by the pelagic living Arctic charr and brown trout.

Predation from fish do also affect the vertical distribution and migration in zooplankton, and the species with the most pronounced vertical migration, *B. longispina*, is strongly affected by predation from fish (Dervo, 1988, Saksgård & Hesthagen, 2004). Despite strong fish predation on *H. gibberum* and *D. longispina* vertical migration are lacking in some years. They have to choose between two contradictory interests, to escape predation or grow and reproduce (Stich & Lampert, 1984; Johnsen & Jakobsen, 1987). Reducing vertical migration in order to stay in the layer with the best food conditions, is probably necessary in lakes of low productivity such as Lake Atnsjøen (Johnsen & Jakobsen, 1987). When the food concentrations increase it becomes more profitable to migrate, as demonstrated for example in 1988 and 1990.

C. scutifer is the only invertebrate predator occurring in any high density. *H. saliens* and *B. longimanus* are also predators, but occur in very low densities. *C. scutifer* is supposed to be omnivorous (Larsson, 1978; Langeland & Reinertsen, 1982) and is able to survive, grow and reproduce utilising allochthonous material (Taube & Nauwerck, 1967). The nauplii and small copepodites are macrofiltrators, while Cop. IV–

V and the adults are seizers and carnivorous. Potential target animals are rotifers, nauplii, small copepodites and small cladocerans (*B. longispina*) (Gliwicz, 1974; Larsson, 1978; Nilssen, 1978). Cannibalism is likely.

The same three species of rotifers dominate in Lake Atnsjøen as in Lake Øvre Heimdalsvatn (Larsson, 1978). Low densities in spring, and sometimes also in autumn indicate that they pass the winter mainly as resting eggs, but they do also occur in low densities in the water column during winter. In Lake Øvre Heimdalsvatn they pass the winter in quite high densities, and in *K. longispina* no production of resting eggs has been observed.

The calanoid copepod *A. laticeps* usually occurs in low to very low densities, and it is not possible to estimate the number of generations in Lake Atnsjøen with any certainty. The rarity of calanoid copepods in Lake Atnsjøen is difficult to explain, but competition for food, low food concentration and high through-flow, are probably among the reasons. *A. laticeps* is a filtrator and will compete for food with the cladocerans, and also with the nauplii and small copepodites of *C. scutifer*. In Øvre Heimdalsvatn filtering calanoids are also lacking (Larsson, 1978), and they are also almost lacking in the alpine lakes Gjende and Bessvatn (Elgmork & Eie, 1989). Calanoids are, however, common and able to survive under similar environmental conditions in other lakes (Shiel et al., 1982; Much & Lampert, 1984; Ferrari et al., 1989; Pace et al., 1992; Thorpe et al., 1994) and it may therefore be speculated that food conditions are too poor in Lake Atnsjøen, and that calanoids are not able to survive on allochthonous material alone.

The seasonal occurrence indicate two generations per year both in *B. longispina* and *D. longispina*, and maybe also in *A. laticeps* and *H. gibberum*. It is, however, difficult to determine the number of generations based on densities only, especially when number of sampling series are as low as five during summer.

In *A. laticeps* two main types of life cycles are common, one where the population pass the winter mainly as resting eggs, as in Lake Atnsjøen (Lötmarker, 1964), and one where it pass the winter as copepodites and where noticeable growth occur during winter (Jensen, 1981; Nøst & Jensen, 1997).

In Lake Øvre Heimdalsvatn *H. gibberum* and *B. longispina* had three and four generations per year, respectively (Larsson, 1978), and they over-wintered as resting eggs. The same is documented in many other lakes. *H. gibberum* is never found during winter, while both *B. longispina* and *D. longispina* may reproduce

below the ice, even in alpine lakes (Halvorsen, 1973; Allan, 1977; Vijverberg, 1980; Schartau, 1985; Skov, 1985). The fewer generations in Lake Atnsjøen compared with Lake Øvre Heimdalsvatn may be explained by poorer food conditions. The somewhat prolonged lifecycle in *C. scutifer* support this idea.

The observed life cycle in *C. scutifer*, with a large fraction using one year from egg to adult, and a small fraction using two years, is very common in oligotrophic lakes (Axelson, 1961; Halvorsen & Elgmork, 1976; Larsson, 1978; Elgmork, 1985; Nøst & Jensen, 1997). The size of the two year fraction varies between localities, and between years, from zero to near 100% of the population. In high alpine lakes the life span from egg to adult can be even longer, up to three years (Elgmork & Eie, 1989).

It is well known that high through-flow reduce zooplankton density, especially during high flood periods (Shiel & Walker, 1984; Larsson, 1978). This is also the case in Lake Atnsjøen where the density is very low after the spring flood. Occasionally floods throughout the year also reduce plankton densities. We have, however, not been able to demonstrate any significant correlation between zooplankton density and discharge, indicating that this correlation may be masked by other factors.

Large horizontal and vertical variation in both phyto- and zooplankton densities are observed in the lake, with highest densities towards the outlet (Fagernæs, 1989; Dervo, 1988), which partly can be explained by high through-flow and local differences in currents. Lake Atnsjøen is strongly affected by wind. Strong currents down to at least 20–30 m depth are observed.

The high mortality of *C. scutifer* during winter, in some years almost 94% of the population disappear, is probably related to high through-flow. The special high mortality during the winter 1994/1995 corresponds with the especially high water flow in spring 1995. The through-flow cannot, however, explain the low mortality during the winter 1989/1990. In general, we found no significant correlation between survival and through-flow. Predation from fish may affect winter survival, but *C. scutifer* is rarely taken by fish, and in winter fish predation is also generally low.

High dominance of rotifers is an indication of high through-flow (Shiel & Walker, 1984), which was clearly demonstrated after the high flood in 1995 (Brabrand, 1998). The density of rotifers increased threefold after the flood while the increase in cladocerans and copepods were smaller. The dominance of

rotifers over crustaceans, is largely caused by the more rapid reproduction in rotifers.

Summary

The Lake Atnsjøen has been studied during the period 1985–1997 (Fig. 1). From 1985 to 1988 the material was sampled from 6 stations, three stations along the lake (St. B1, B2 and B3), and three stations across the lake outside Sørnesset (St. A1, C1 and D1). From 1989 the sampling has been reduced to only three stations (B1, C1, D1). The sampling program has been standardised since 1989. Sampling was done five times during the ice-free period from June to October.

The number of species observed in Lake Atnsjøen is 37, 17 species of Rotatoria, 9 species of Copepoda, and 11 species of Cladocera (Table 2). Of these 10 species of Rotatoria, five species of Cladocera and two species of Copepoda occur regularly and relatively numerous. The species composition has varied only slightly during the study. All species are widely distributed in Southern Norway. The plankton community in Lake Atnsjøen is typical for oligotrophic, high altitude lakes.

The share of rotifers has increased since 1991 (Fig. 2). In the period 1985–1990 they constituted less than 15% of the individuals at the beginning of June, while they at the same time during 1991–1997 constituted between 30% and 80%. The first six years there was a relatively strong dominance by copepods in spring and early summer. The cladocerans usually constituted less than 10–15% of the individuals.

The maximum density of the plankton has varied from about 50 ind. l^{-1} (1985, 1988) to nearly 400 ind. l^{-1} (1995) (Fig. 3). Usually the density vary about 150 ind. l^{-1} (1990–1994, 1989). The plankton community was dominated by rotifers, with up to more than 10–15 times the density of cladocerans and copepods together. The density of the copepods was about twice as high as that of the cladocerans.

The density is low in spring. The mortality during winter can be very high in winter-active species, up to 94% (Fig. 2). Most species are, however, passing the winter as resting eggs.

Maximum density, mainly correlated to rotifers, occur either at the beginning of July (1986, 1992, 1993), at the end of August (1990, 1991, 1994, 1995) or at the end of September (1987, 1989). Low and even density throughout the season is observed in 1985 and 1988. There seems to be no significantly correla-

tion, either directly or indirectly, between community structure and variations in temperature, water through-flow, food conditions, predation, and competition. The zooplankton community in lake Atnsjøen seems, however, to be highly dependent on allochthonous material.

The rotifers are dominated by *P. vulgaris*, *K. longispina* and *C. unicornis* (Fig. 5), whereas all the other species normally constitute less than 20% of the community. *K. longispina* is quite numerous in spring, while *P. vulgaris* take over later in summer and autumn. *P. vulgaris* dominate during the time of maximum density except in 1985 when *C. unicornis* constituted about 50%.

The crustaceans are dominated by *C. scutifer*, *B. longispina*, *D. longispina* and *H. gibberum*, with *C. scutifer* and *B. longispina* as the most numerous (Fig. 7). The low densities of *H. saliens*, *D. longispina*, and *H. gibberum* may be caused by predation from fish.

The life cycle of *Cyclops scutifer* show great similarities during the period from 1991 to 1997 (Fig. 9), while the life cycle in 1989 and 1990 differ quite strongly from the other years. The main reproduction occur in July to September, the time may vary somewhat from year to year. The first nauplii appear in the beginning of July, but large numbers appear in the beginning of August. The main population have a one year life cycle, while a small fraction need about two years before reproducing. It pass the winter mainly as large nauplii and small copepodites.

Bosmina longispina dominate among the cladocerans (Fig. 10). Maximum density vary between less than 5 ind. l^{-1} to nearly 40 ind. l^{-1} . The development vary from year to year without any common features. The share of females with eggs (F_{ov}) is low, and there is no correlation between number of egg per female and variation in density. Males of *B. longispina* appear in August, with maximum occurrence in September. The first resting eggs are observed in August, and the main population pass the winter as resting eggs.

Daphnia longispina occur in low densities, between less than 1 ind. l^{-1} to nearly 7 ind. l^{-1} (Fig. 11). There are a small maximum in the beginning of July and a somewhat larger one in the beginning of September. They pass the winter as resting eggs. The population is dominated by females without eggs (F). There is no clear correlation between number of females with eggs (F_{ov}) and variations in density. Males is observed only in small numbers.

H. gibberum occur in low densities, not exceeding 2–3 ind. l⁻¹ (Fig. 12). It is a summer form and is most common in June and July. It pass the winter as resting eggs. The population have only one maximum, usually in July. Males are not observed.

Arctodiaptomus laticeps occur only in low densities (Fig. 13), from less than 0.1 ind. l⁻¹ to about 4 ind. l⁻¹. It pass the winter mainly as resting eggs. The time of highest density vary from July to September.

The material indicate two generations per year in both *B. longispina* and *D. longispina*, and probably also in *A. laticeps* and *H. gibberum*.

The plankton community have highest density between 5–10 m depth during the day (Fig. 14). The depth of highest density increase during summer in accordance with the lowering of the thermocline and increasing transparency. The rotifers occur closer to the surface than the crustaceans, while the copepods occur deeper than the cladocerans. The vertical migration is pronounced during day and night, especially in *Bosmina longispina*. The main part of the zooplankton community occur near the surface during night (Fig. 15). Predation from fish, brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*), are probably one important reason for this vertical distribution and migration.

There are observed only weak correlation between environmental factors and the development of the zooplankton community. More complex, multifactorial analyses are necessary to reveal possible correlation between the environmental factors and the development of the zooplankton community.

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Annual variability in the life-history characteristics of brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) in a subalpine Norwegian lake

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Key words: time series, brown trout, Arctic charr, life history, inter-cohort variation

Abstract

The annual variability in growth and life history traits of brown trout (*Salmo trutta* L.) and Arctic charr (*Salvelinus alpinus* (L.)) in Lake Atnsjøen, a Norwegian subalpine lake, was studied over a period of 13 years (1985–1997). The extent to which life-history characteristics recorded on one occasion can be regarded as representative for the population was explored. We found inter-cohort variation in growth for both species; estimates of asymptotic length (L_{∞}) in ten cohorts ranged between 225–305 mm ($CV = 10.5\%$) for brown trout and 273–301 mm ($CV = 4.1\%$) for Arctic charr. However, this variation was much lower than inter-population variation for brown trout based on single samples from 169 populations ($CV = 24.6\%$). In Lake Atnsjøen, annual growth increment correlated highly with the number of days warmer than 7 °C ($R^2 = 0.60–0.89$) for brown trout, and days warmer than 10 °C ($R^2 = 0.40–0.58$) for Arctic charr. Females of Arctic charr were younger at sexual maturity than males, while no such difference was found in brown trout. Generally speaking, early maturing individuals of both species grew faster, particularly from age-2 and onwards, than immature individuals. Early maturing individuals, however, were smaller at maturity than those maturing one year older. Age and size at maturity were significantly correlated with asymptotic lengths only in Arctic charr females.

Introduction

Most teleost fishes exhibit indeterminate and plastic growth patterns, and both growth rate and maximum body size are strongly influenced by environmental conditions (Weatherley & Gill, 1987). Therefore, growth may vary considerably among fish populations of the same species. This may be due to the direct influence of environmental factors (Jonsson et al., 1984), i.e. phenotypic plasticity, or to genetic adaptations to local environmental conditions (Fleming & Gross, 1989). This plasticity translates into large variation in life history characteristics, which is well documented among fish populations in a variety of species (Schaffer & Elson, 1975; Leggett & Carscadden, 1978; Scarnecchia, 1983; Fleming 1996). How-

ever, few long-term studies have been conducted that describes the temporal within-population variability in life history characteristics such as growth rate and age and size at maturity. Therefore, it is largely unknown to what extent life history characteristics based on samples from one year or one occasion, can be regarded as representative for the specific population.

In fishes, the two main environmental factors expected to result in large inter-annual variability in growth are water temperature and food availability (Jensen, 1977; Amundsen & Klemetsen, 1988; Hesthagen et al., 1995). Inter-annual variability in growth may also influence the age and size at sexual maturity because fast-growing individuals mature at a younger age and smaller body size than more slow-growing ones (Alm, 1959; Thorpe, 1986; Jonsson

et al., 1984; Stearns, 1992; Forseth et al., 1994). Thus, estimates of growth, and age and size at sexual maturity, are valuable variables for describing the population status in undisturbed fish populations.

When using life history traits in fish species as biological indicators in monitoring freshwater systems, it is important to know the natural intra-population variability of the life history variables, in order to separate natural and anthropogenic variation. However, few long-term studies have described the annual variability in life history characteristics within specific populations, and little is known about the value of single samples in characterising a population. In this study we investigated the annual variability in growth rate and age and size at sexual maturity of brown trout (*Salmo trutta* L.) and Arctic charr (*Salvelinus alpinus* (L.)) in a subalpine Norwegian lake based on data for 13 years.

Material and methods

Study area

The study was carried out in the unregulated Lake Atnsjøen (surface area: 4.8 km²) in south-eastern Norway. The lake is located at 701 m a.s.l., and is usually ice-free from late May to mid November. The lake is oligotrophic and slightly acid, with a pH and calcium content that usually range between 6.0–6.6 and 0.5–1.0 mg l⁻¹, respectively (Blakar et al., 1997). The Secchi depth typically ranges between 9–10 m. However, in the spring of 1995 there was an extraordinarily high flood (Tvede, 2004), and the Secchi depths temporarily dropped to 3.5 m (Austigard & Holmedal, 1998). Such high floods are expected to occur at intervals of between 100–200 years (Erichsen, 1995). The lake is relatively deep with mean and maximum depths of 35 and 80 m, respectively (Østrem et al., 1984). In addition to brown trout and Arctic charr, Lake Atnsjøen contains Siberian sculpin (*Cottus poecilopus* (HECKEL)) and European minnow (*Phoxinus phoxinus* (L.)) (Hesthagen & Sandlund, 2004). Siberian sculpin are regularly found in epibenthic habitats at depths between 5–20 m (Austigard & Holmedal, 1998), while the abundance of European minnow is very low. The most important spawning areas for brown trout in Lake Atnsjøen are in the inflowing River Atna, below Liafossen waterfall (10–14 km upstream of Lake Atnsjøen). Stretches closer to the lake (0–10 km) have a fine substrate unsuitable for brown trout spawning. Brown trout also

spawn in a small area at the outlet (limited by a waterfall) and in several tributary streams. Arctic charr spawn in the littoral zone at different locations in the lake only.

Sampling and analyses

Fish were sampled with benthic and pelagic gill nets between 10–20 August during 13 consecutive years between 1985 and 1997. From 1985 to 1994, series of benthic gill nets (25 m long and 1.5 m deep) with mesh sizes between 16–45 mm (Jensen, 1977) were set in gangs at depths between 0–10, 10–30 and 30–70 m, respectively (Saksgård & Hesthagen, 2004). From 1994 to 1997, sampling in the epibenthic habitat was carried out with multi-mesh gill nets 30 m in length and 1.5 m in depth, with mesh sizes between 5 and 55 mm (Appelberg et al., 1995). The benthic nets were set at depths of 0–3, 3–6, 6–12, 12–20, 20–35, 35–50 and > 50 m (Saksgård & Hesthagen, 2004). The pelagic nets (25 m long and 6 m deep) were set at depths of 0–6 and 6–12 m, and had mesh sizes of 16–45 mm (1985–1993) and 10–45 mm (1994–1997). The gill nets series used catch fish of lengths between 15 and 30 cm with about equal efficiency (Kurkilahti et al., 2002).

Fish length was measured to the nearest millimetre from the snout to the outer lobes of the tail in natural position (natural tip length), and fish were weighted to the nearest gram. The degree of sexual maturity was recorded according to Dahl (1917), and grouped into immature specimens [stages 1–2] and mature specimens [(stages 3–5 (ripening or ripe), and stage 7 (spent)]. Fish in stage 6 (spawning) were not caught because sampling was carried out before spawning. Age at maturity is defined as the age at which 50% of the fish are sexually mature, which was estimated from linear approximation of the percentage of mature fish in each age group (Vøllestad et al., 1993).

The age of brown trout was determined by means of both scales and sacculus otoliths (Jonsson, 1976), while only otoliths were used to age Arctic charr (Kristoffersen & Klemetsen, 1991). Totals of 2817 Arctic charr and 1363 brown trout were caught of which 2467 (87.6%) and 1326 (97.3%) specimens were age, respectively.

To compare length increment within cohorts and between years, lengths were back-calculated using scales for brown trout and otoliths for Arctic charr. These calculations were made according to a method suggested by Ricker (1992), based on separate calcu-

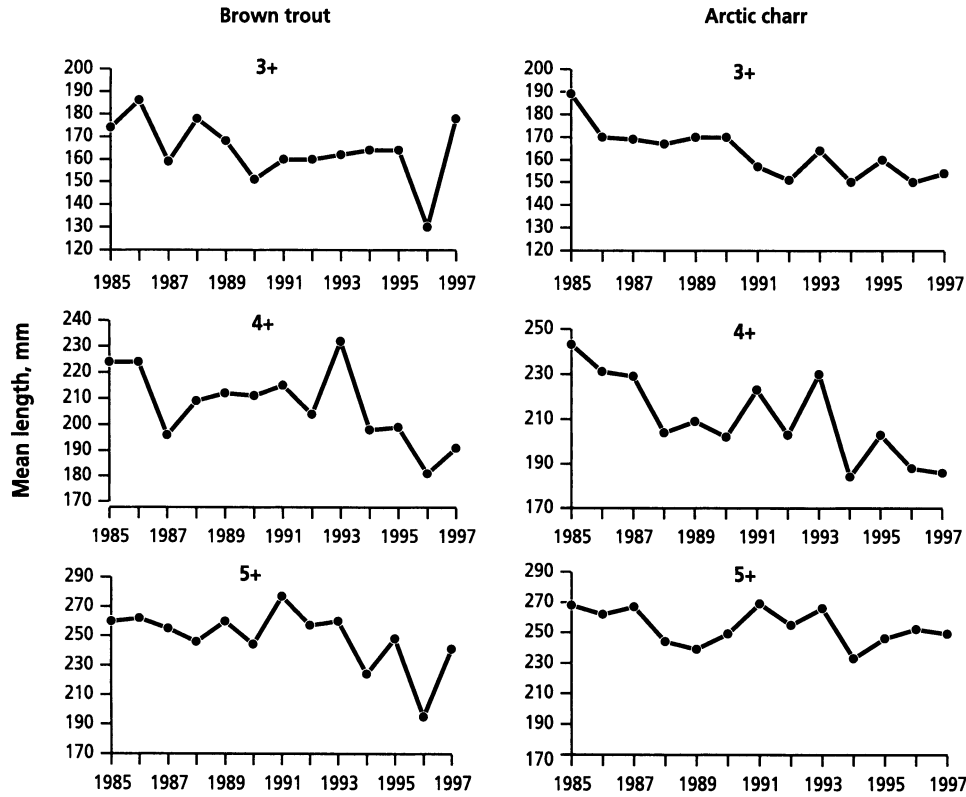


Figure 1. Empirical lengths (mm) of brown trout and Arctic charr in age groups 3–5 in Lake Atnsjøen, 1985–1997.

lations for each sampling year:

$$L_d = \frac{(L_s - k)S_d}{S_r}, \quad (1)$$

where L_d is the length of fish when the d th annulus was formed, L_s is the length of fish at the time of sampling, k is the estimated intercept on the length axis, S_d is the actual distance from the centre of the scale/otolith to the d th annulus, and S_r is the actual radius of the scale or otolith. The intercept on the length axis (k) was estimated by means of geometric mean regression between fish length and scale/otolith radius (both values were \ln transformed).

Differences in back-calculated lengths were tested using ANOVA with the Scheffé *a posteriori* range tests.

The asymptotic length (L_∞) and the rate at which this length is attained, i.e. the growth coefficient (k), were estimated according to a revised version of von Bertalanffy's growth equation (von Bertalanffy, 1938; Allen, 1966), based on empirical length at age data for different cohorts:

$$L_t = L_\infty - (L_\infty - L_{t-1}) \cdot e^{-k \cdot L_t} \quad (2)$$

where L_t is total length at age t and t_0 is the time when length would theoretically be zero. The growth curves were fitted assuming a length at age 0 (i.e. first external feeding) of 18 mm for brown trout (Frost & Brown, 1967) and 20 mm for Arctic charr (Johnson, 1980). The model parameters were estimated by non-linear least square regressions. We used data from different cohorts rather than from different years in these analyses in order to avoid dependency in the data.

The growth increment of brown trout and Arctic charr was studied in relation to the water temperature, which was recorded continually at the outlet of Lake Atnsjøen (Tvede, 2004). The water temperature data from 1990 were excluded as no measurements were made after 1 August. Annual growth was regressed against (i) the number of days with a water temperature that exceeded threshold values between 5 and 10°C, and (ii) mean temperature in different months. In these analyses, growth was represented by the length increment during the last growing season prior to capture using fish at ages 3, 4 and 5 as test groups. Asymptotic lengths estimated from equation 1 were also regressed against the temperature variables.

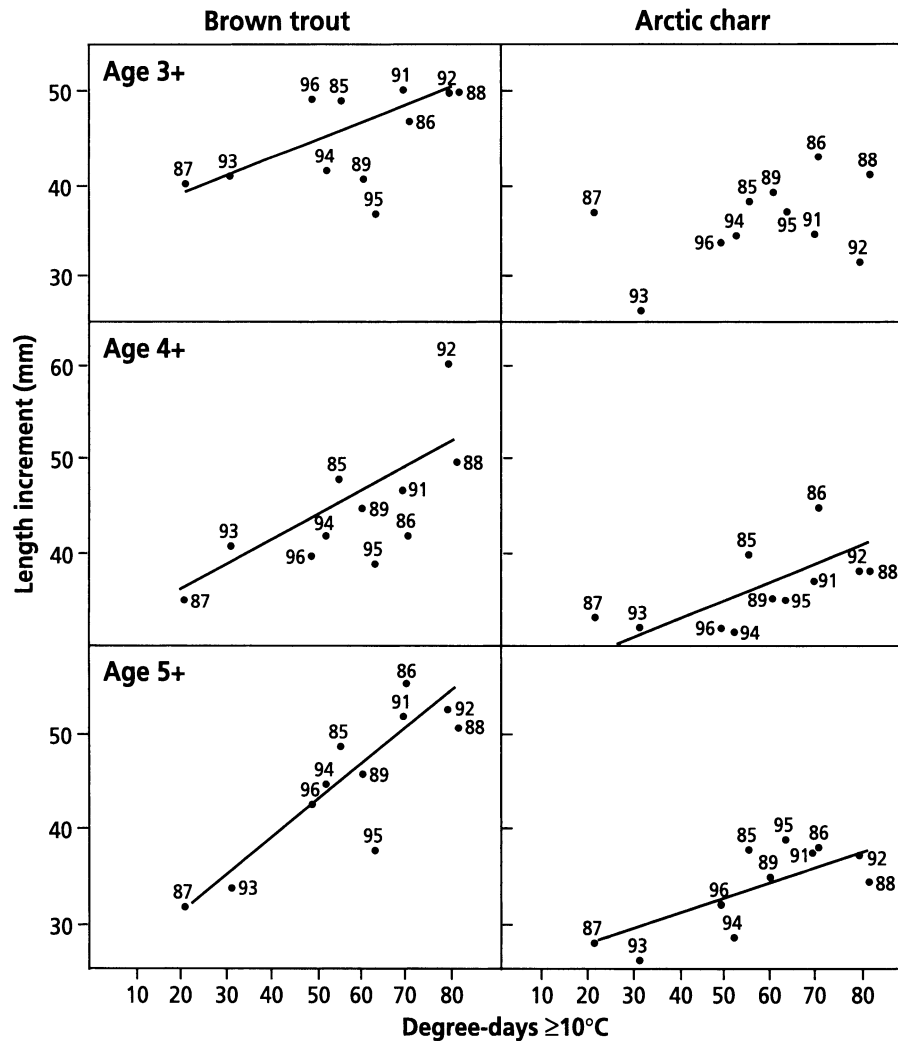


Figure 2. Relationship between length increment (mm) in the last growth season for brown trout (BT) and Arctic charr (AC) of ages 3, 4 and 5 and the number of days with temperatures above 10°C ($\text{TD} \geq 10$) in Lake Atnsjøen, 1985–1997. Lines represent significant ($p < 0.05$) linear regressions and numbers at different points indicate year of investigation. Estimated model parameters (\pm SE) for the best relationships in each age group were (excluding data from 1995): [$\text{BT}_{\text{Age}3}$: $0.16 \pm 0.05 * \text{TD} \geq 10 + 37.08 \pm 3.08$, $R^2 = 0.49$, $p < 0.05$], [$\text{BT}_{\text{Age}4}$: $0.28 \pm 0.08 * \text{TD} \geq 10 + 29.08 \pm 4.95$, $R^2 = 0.54$, $p < 0.01$], [$\text{BT}_{\text{Age}5}$: $0.42 \pm 0.05 * \text{TD} \geq 10 + 22.98 \pm 3.08$, $R^2 = 0.89$, $p < 0.0001$], [$\text{AC}_{\text{Age}4}$: $0.14 \pm 0.06 * \text{TD} \geq 10 + 28.14 \pm 3.44$, $R^2 = 0.36$, $p < 0.05$], [$\text{AC}_{\text{Age}5}$: $0.18 \pm 0.05 * \text{TD} \geq 10 + 23.24 \pm 2.92$, $R^2 = 0.59$, $p < 0.01$].

Results

Growth increment

Both brown trout and Arctic charr exhibited considerable temporal variation in growth rates as indicated by their empirical length at age for fish in age groups 3–5 (Fig. 1). The asymptotic length (L_{∞}) in von Bertalanffy's growth equation differed greatly among cohorts of brown trout (225–306 mm, $\text{CV} = 10.5\%$), but to a lesser extent in Arctic charr (273–310 mm, $\text{CV} = 4.1\%$) (Table 1). Both species also exhibited consid-

erable variation in the growth coefficient (k), ranging between 0.53–0.77 in brown trout ($\text{CV} = 12.2\%$) and 0.48–0.66 in Arctic charr ($\text{CV} = 10.0\%$), respectively. Asymptotic length and the growth coefficient were highly correlated in different cohorts of brown trout: ($R^2 = 0.81$, $F_{1,8} = 39.7$, $p < 0.0001$), but to a lesser extent in Arctic charr ($R^2 = 0.30$, $F_{1,8} = 4.8$, $p = 0.059$).

Lake Atnsjøen exhibits relatively small annual variation in water temperature during late autumn and winter, as is indicated by the variation in the number

Table 1. Growth coefficients ($k \pm \text{SE}$) and asymptotic lengths (L_{∞} , mm $\pm \text{SE}$) of the 1983–1992 cohorts of brown trout and Arctic charr in Lake Atnsjøen, 1983–1992. Regression coefficients (R^2) and number of age groups used in the modelling (N) are given.

Cohort	Brown trout				Arctic charr			
	k	L_{∞}	N	R^2	k	L_{∞}	N	R^2
1983	0.60 ± 0.06	296 ± 1.1	7	0.99	0.66 ± 0.06	276 ± 1.1	7	0.99
1984	0.60 ± 0.08	292 ± 1.1	6	0.99	0.61 ± 0.07	282 ± 1.1	6	0.99
1985	0.55 ± 0.03	304 ± 1.1	7	0.99	0.54 ± 0.07	281 ± 1.1	7	0.98
1986	0.59 ± 0.06	300 ± 1.1	7	0.99	0.61 ± 0.05	291 ± 1.1	8	0.99
1987	0.58 ± 0.07	296 ± 1.1	5	0.99	0.55 ± 0.04	301 ± 1.0	7	0.99
1988	0.53 ± 0.04	306 ± 1.1	6	0.99	0.50 ± 0.06	290 ± 1.1	8	0.99
1989	0.72 ± 0.12	257 ± 1.1	6	0.99	0.48 ± 0.07	310 ± 1.1	8	0.98
1990	0.60 ± 0.08	265 ± 1.1	7	0.99	0.59 ± 0.08	273 ± 1.1	7	0.99
1991	0.67 ± 0.09	239 ± 1.1	5	0.99	0.58 ± 0.13	276 ± 1.2	6	0.98
1992	0.77 ± 0.11	225 ± 1.1	5	0.99	0.52 ± 0.08	285 ± 1.2	4	0.99

Table 2. Observed mean lengths (mm $\pm \text{SD}$) at different ages of sexually immature (SI) and sexually mature (SM) males and females of brown trout and Arctic charr caught in Lake Atnsjøen, 1985–1997. Superscript figures indicate numbers of fish in each group.

Age	Brown trout				Arctic charr			
	Males		Females		Males		Females	
	SI	SM	SI	SM	SI	SM	SI	SM
1	83 ± 09^5		83 ± 15^2		79 ± 04^{13}		78 ± 5^{13}	
2	133 ± 18^{82}		127 ± 15^{68}		110 ± 16^{114}		111 ± 15^{88}	
3	169 ± 22^{196}	205 ± 20^2	164 ± 22^{193}		162 ± 24^{394}		159 ± 23^{270}	182 ± 5^2
4	209 ± 27^{163}	222 ± 21^8	210 ± 30^{165}	215 ± 44^4	217 ± 38^{292}	219 ± 49^9	209 ± 37^{271}	230 ± 37^{12}
5	233 ± 35^{65}	268 ± 24^{19}	247 ± 36^{91}	283 ± 24^{18}	259 ± 33^{204}	243 ± 42^{20}	249 ± 37^{197}	265 ± 25^{60}
6	267 ± 32^{37}	278 ± 29^{28}	270 ± 25^{45}	288 ± 18^{29}	275 ± 36^{75}	281 ± 27^{39}	251 ± 42^{44}	278 ± 28^{113}
7	256 ± 44^9	282 ± 14^6	293 ± 30^{21}	312 ± 27^{15}	285 ± 30^{24}	291 ± 35^{35}	286 ± 21^{18}	290 ± 17^{70}
8	319 ± 09^3	306 ± 43^7	290 ± 13^9	328 ± 38^7	257 ± 47^2	289 ± 43^{14}	286 ± 15^8	281 ± 33^{22}
9		329 ± 14^2	299 ± 17^3		263 ± 59^3	255 ± 47^6	285 ± 00^1	234 ± 52^6
10			335 ± 42^2	540 ± 00^1		254 ± 24^3	305 ± 28^2	276 ± 10^2
11						280 ± 35^2	230 ± 35^1	354 ± 11^2
12			300 ± 00^1			387 ± 00^1		239 ± 52^1

of days each year with temperatures warmer than 5 °C (127–156 days, CV = 5.1%). However, variation in temperature was much larger during the summer, and the number of days warmer than 10 °C ranged between 21 and 81 (CV = 31.4%).

There was a positive correlation between several of the temperature variables and growth (annual length increment) in both brown trout (age 4 vs. days warmer than 6–10 °C, and age 5 vs. days warmer than 7–10 °C) and Arctic charr (age 4 vs. days warmer than 10 °C, and age-5 vs. days warmer than 8–10 °C, all tests: $p < 0.05$). However, if the data from the extraordinary year of 1995 were omitted (with high flooding, see Discussion), the relationship between

water temperature and growth rate was improved (Fig. 2, all tests: $0.05 > p > 0.001$). For brown trout, the best correlation existed between the growth at age 5 and days warmer than 7 °C ($F_{1,8} = 71.6$, $R^2 = 0.89$, $p < 0.001$). For Arctic charr, the best correlation was found between growth at age 5 and days warmer than 10 °C ($F_{1,8} = 13.7$, $R^2 = 0.60$, $p = 0.006$).

The only positive correlation between annual growth increment and the mean water temperature in a single month in corresponding years was found for June. The mean water temperature in this month ranged between 5.0–10.9 °C (CV = 21.2%), and was significantly correlated to brown trout growth at age 4 ($F_{1,10} = 14.7$, $R^2 = 0.55$, $p < 0.005$) and age 5

($F_{1,10} = 9.6$, $R^2 = 0.44$, $p < 0.05$), and Arctic charr growth at age 4 ($F_{1,10} = 8.1$, $R^2 = 0.39$, $p < 0.05$) (Fig. 3).

In Arctic charr, there was a significant positive correlation between asymptotic length and the number of days with temperatures above 7°C during their fourth year of life ($F_{1,6} = 15.6$, $R^2 = 0.68$, $p < 0.01$). No similar correlation was found for brown trout. Moreover, there was no correlation between the asymptotic lengths of Arctic charr and brown trout ($p > 0.05$).

Sexual maturity

In brown trout, a few males became sexually mature at age 3 (1.0%), while the first females matured when they were a year older (2.4%) (Table 2, Fig. 4). The proportion of mature females reached its maximum at ages 6–8 (40–45%), while males peaked at 100% at age 9. The average age at sexual maturity was 6.1 years in females (5.0–8.0 years) and 5.8 years in males (5.0–7.3 years), which was not significantly different (t -test, $p > 0.05$). Brown trout females exhibited a significant annual variation in mean age at maturity (ANOVA, $p < 0.005$), whereas males did not (ANOVA, $p = 0.065$). In females, the mean length at maturity of individual cohorts was significantly correlated with the asymptotic length ($F_{1,6} = 27.9$, $R^2 = 0.82$, $p < 0.05$).

A few females of Arctic charr were sexually mature at age 3 (0.7%), and the proportion increased with age to nearly 90% at age 8. Arctic charr males started to mature at age 4 (3.0%), and the highest proportion was reached at age 7 (80%). The average age at sexual maturity was significantly lower for females than for males (t -test, $p = 0.05$), at 6.3 (range 4.9–7.6) and 6.6 years (range 5.8–8.0), respectively (Table 3). Arctic charr females exhibited a significant annual variation in mean age at maturity (ANOVA, $p < 0.0001$), whereas males did not (ANOVA, $p = 0.068$). There was no significant correlation between the mean size at maturity and asymptotic length of individual cohorts in female Arctic charr ($p > 0.05$).

Mature brown trout individuals had generally larger body size than immature specimens in different age groups (Table 4), and at ages 4–6 the differences were in most cases significant (Scheffé-test, $p < 0.05$). Among Arctic charr, similar differences were only found between mature and immature females at age 5 and 6. In both species, the general picture was that early maturing individuals in a cohort were smaller at

maturity than those that matured one year older. When sufficient numbers of fish were available to allow for statistical analyses (Arctic charr only), this difference was always significant (t -tests, $p < 0.05$).

Discussion

The asymptotic length (L_{∞}) in von Bertalanffy's growth equation showed greater variability among cohorts of brown trout (CV = 10.5%) than of Arctic charr (CV = 4.1%). The variability was lower than that found for different populations of the two species on the basis of Ford–Walford plots and samples from one year (Vøllestad et al., 1993; Vøllestad & L'Abée-Lund, 1994). Analyses of growth data from 169 populations of brown trout in Norwegian lakes using the same analytical approach as employed in this study gave CV values for asymptotic length of 24.6% (Ola Ugedal, personal communication). The relatively low intra-cohort variation in Arctic charr and brown trout in Lake Atnsjøen, indicates that estimates of asymptotic length based on a single round of sampling can be regarded as representative of the particular population. This is particularly the case for Arctic charr. Moreover, the much lower variability found within than among populations, show that proper estimates based on single samples can be used for comparisons of growth traits across populations. However, when considering inter-population variability in growth, i.e. fish populations from different geographic regions, a genetic component in relation to growth rate should not be excluded (Palm & Ryman, 1999).

We found some indications that temperature influences asymptotic lengths (L_{∞}) of Arctic charr, as this parameter was significantly correlated to the number of days with temperatures above 7°C during their fourth year of life. At this age maturation is initiated and growth generally slows down. Therefore, it appears reasonable that growth rate during the last year prior to maturation may influence the asymptotic length attained. A similar relationship was not found for brown trout, and the asymptotic lengths of Arctic charr and brown trout did not correlate. These results indicate that the maximum size of the two species is not strongly influenced by a common environmental factor such as temperature. Due to differences in habitat use between Arctic charr and brown trout in Lake Atnsjøen (Austigard & Holmedal, 1998; Saksgård & Hesthagen, 2004), their thermal environment may be quite different, although correlated.

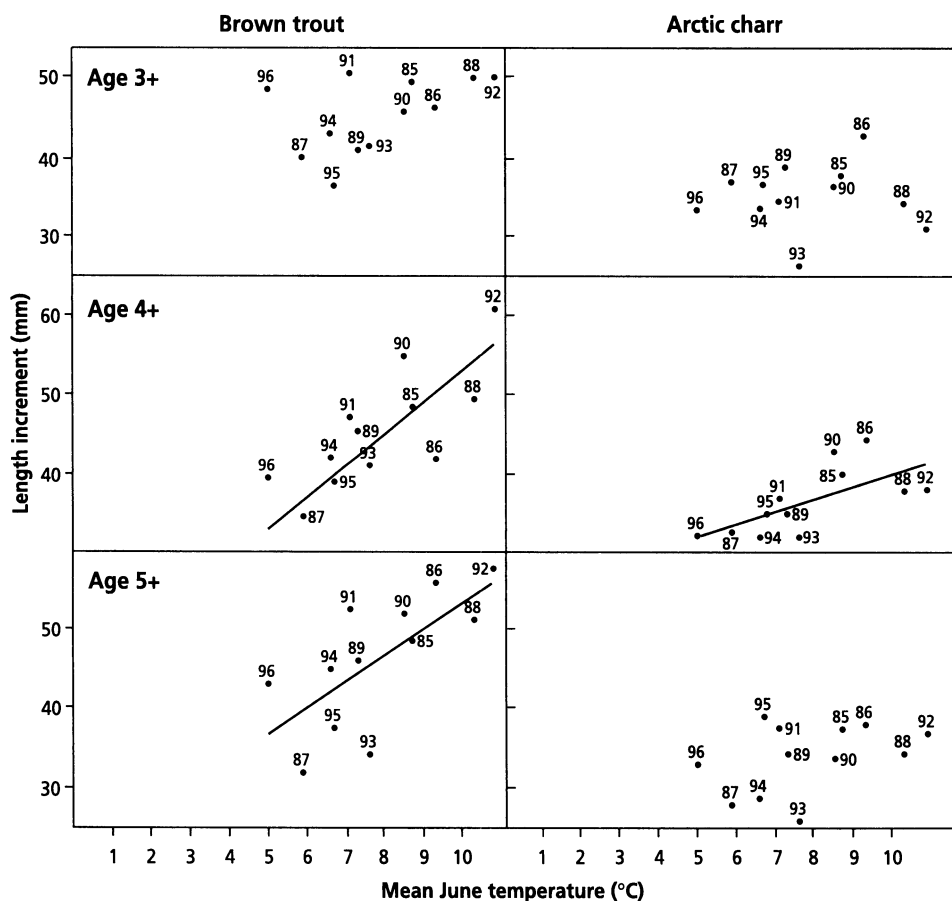


Figure 3. Relationship between length increment (mm) in the last growth season for age groups 3+, 4+ and 5+ of brown trout (BT_{Age3-5}) and Arctic charr (AC_{Age3-5}) and mean water temperature in June (T_J) in Lake Atnsjøen, 1985–1997. Lines represent significant ($p < 0.05$) linear regressions and numbers at different points indicate year of investigation. Estimated model parameters (\pm SE) for the best relationships in each age group were (excluding data from 1995): [BT_{Age4} : $3.24 \pm 0.85 * T_J + 20.081 \pm 6.77$, $R^2 = 0.56$, $p < 0.005$], [BT_{Age5} : $3.34 \pm 1.08 * T_J + 20.25 \pm 8.61$, $R^2 = 0.44$, $p < 0.05$], [AC_{Age4} : $1.66 \pm 0.58 * T_J + 23.63 \pm 4.66$, $R^2 = 0.39$, $p < 0.05$].

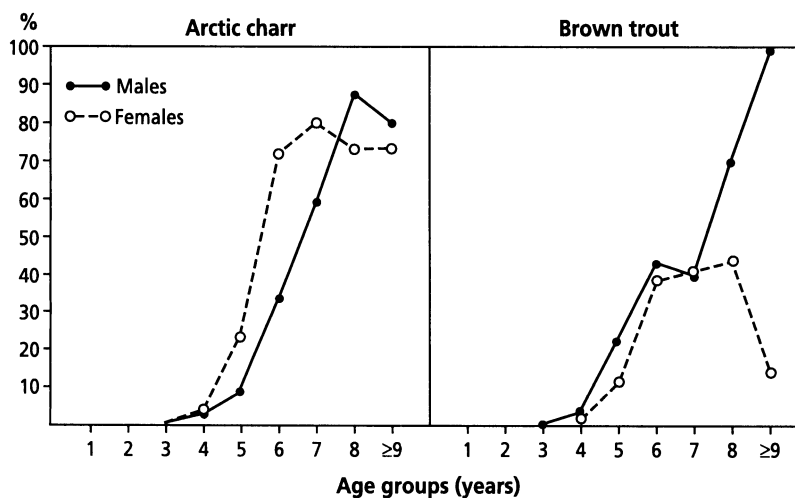


Figure 4. The proportion of sexually mature males and females of different age classes of Arctic charr and brown trout in Lake Atnsjøen, 1985–1997.

Table 3. Mean age at maturity (\pm SD) of males and females of brown trout and Arctic charr in Lake Atnsjøen, 1985–1997. Number of fish in parenthesis.

Year	Brown trout		Arctic charr	
	Males	Females	Males	Females
1985	5.67 \pm 0.33 (3)	6.08 \pm 0.23 (12)	5.88 \pm 0.26 (17)	6.44 \pm 0.14 (59)
1986	6.00 \pm 0.50 (8)	5.90 \pm 0.28 (10)	7.27 \pm 0.52 (11)	6.10 \pm 0.16 (30)
1987	6.33 \pm 0.33 (3)	7.00 \pm 0.00 (2)	6.50 \pm 0.43 (6)	6.22 \pm 0.19 (23)
1988	5.60 \pm 0.51 (5)	6.70 \pm 0.30 (10)	6.17 \pm 1.08 (6)	6.87 \pm 0.30 (8)
1989	5.36 \pm 0.43 (11)	6.25 \pm 0.31 (8)	6.55 \pm 0.37 (11)	5.82 \pm 0.18 (38)
1990	5.60 \pm 0.24 (5)	7.00 \pm 1.00 (4)	5.80 \pm 0.44 (10)	5.91 \pm 0.17 (23)
1991	5.00 \pm 0.41 (4)	5.00 \pm 0.17 (12)	7.00 \pm 0.97 (6)	6.61 \pm 0.32 (18)
1992	7.25 \pm 0.53 (8)	7.00 \pm 1.00 (2)	8.00 \pm 0.58 (3)	6.67 \pm 0.88 (3)
1993	5.20 \pm 0.58 (5)	5.92 \pm 0.36 (12)	5.75 \pm 0.25 (4)	4.90 \pm 0.25 (21)
1994	6.75 \pm 0.95 (4)	8.00 \pm 0.00 (1)	7.00 \pm 0.44 (13)	7.58 \pm 0.48 (12)
1995	5.25 \pm 0.37 (8)	7.00 \pm 0.00 (1)	6.23 \pm 0.23 (26)	6.58 \pm 0.38 (24)
1996	6.00 \pm 0.00 (3)		7.42 \pm 0.51 (12)	6.84 \pm 0.38 (19)
1997	5.40 \pm 0.24 (5)		7.00 \pm 0.00 (4)	6.94 \pm 0.35 (16)
Mean	5.79 \pm 0.15 (72)	6.09 \pm 0.1 (74)	6.55 \pm 0.13 (129)	6.29 \pm 0.08 (294)

As expected, annual growth increments were strongly correlated to temperature conditions. However, the strength of the relationships varied among age-groups and between the species. The relationship between annual length increment and temperature, expressed as the number of days warmer than 5–10 °C, were generally weaker for small than for large brown trout, and also weaker for Arctic charr than for brown trout. The growth of young and small brown trout may be more influenced by competition for food and space than older and larger individuals. Consequently, the relative importance of temperature is less. All age groups of brown trout in Lake Atnsjøen tend to occupy the shallow areas close to shore (Hegge et al., 1989; Austigard & Holmedal, 1998; Saksgård & Hesthagen, 2004). The lake has a narrow littoral zone, and only the uppermost 5 m are covered with stones that provide shelter for fish. Young and small fish are competitively inferior to larger individuals, and the effect of intraspecific competition for food and space among brown trout is probably strongest in young fish. The weaker relationship between water temperature and growth in Arctic charr than in brown trout is probably partly due to inadequate temperature measurements for this species. Water temperature was measured in surface waters at the lake outlet, which is within the main habitat zone for brown trout, while Arctic charr generally stay deeper, and in colder water (Austigard & Holmedal, 1998; Saksgård & Hesthagen, 2004). However, when Arctic charr reach a length of about 23 cm

they may utilise the pelagic zone during the ice-free season (Hegge et al., 1989; Saksgård & Hesthagen, 2004).

The growth rate of brown trout in 1995 was much lower than expected on the basis of water temperatures that year, while Arctic charr showed normal growth. We suggest that this reduction in brown trout growth was due to the exceptionally large flood which reduced the abundance of their main food base, i.e. benthic invertebrates (cf. Saksgård & Hesthagen, 2004). The reduced abundance of benthic organisms in Lake Atnsjøen in 1995 (Aagaard et al., 1997), was probably due to heavy sedimentation caused by the flood. On the other hand, Arctic charr in Lake Atnsjøen mainly feed on a range of zooplankton species such as *Bosmina longispina* and *Daphnia longispina* (Austigard & Holmedal, 1998; Saksgård & Hesthagen, 2004). The abundance of these organisms was little affected by the flood (Halvorsen & Papinska, 1997; Halvorsen et al., 2004).

As the growth rate of fish changes, a reproductive adjustment through changes in age and size at maturity is normally observed (Jonsson et al., 1984). Juvenile growth rate appears important in determining the age at first maturity of Arctic charr and brown trout in Lake Atnsjøen, as early maturing individuals grew faster and thus were larger than immature specimens at any specific age. Early maturing individuals, however, were smaller at maturity than those maturing the following year; one year older. These differences in

Table 4. Back-calculated lengths (L1–L6) in mm (mean \pm SD) at ages 1–6 of sexually mature (SM) and sexually immature (SI) males (M) and females (F) in age groups 4–6 of brown trout (BT) and Arctic charr (AC) caught in Lake Atnsjøen, 1985–1997. The mean lengths of the various age groups were tested for significant differences with an ANOVA, Scheffé multiple range test. Mean values in each column followed by different superscript letters are significantly different ($p < 0.05$). N = number of fish.

Species	Sex	Stage	N	Age	L1	L2	L3	L4	L5	L6
BT	M	SM	8	4	39 \pm 11	82 \pm 16	135 \pm 17	192 \pm 23		
	M	SI	160	4	39 \pm 8	84 \pm 15	128 \pm 19	174 \pm 29		
	F	SM	3	4	40 \pm 12	90 \pm 9	139 \pm 15	214 ^a \pm 4		
	F	SI	163	4	40 \pm 9	86 \pm 15	131 \pm 21	175 ^b \pm 28		
	M	SM	17	5	41 \pm 9	89 ^a \pm 9	140 ^a \pm 13	193 ^a \pm 20	242 ^a \pm 24	
	M	SI	62	5	37 \pm 9	77 ^b \pm 16	118 ^b \pm 20	159 ^b \pm 28	202 ^b \pm 33	
	F	SM	18	5	39 \pm 10	90 ^a \pm 17	156 ^a \pm 62	201 ^a \pm 28	255 ^a \pm 24	
	F	SI	87	5	39 \pm 9	80 ^b \pm 16	125 ^b \pm 22	168 ^b \pm 28	213 ^b \pm 33	
	M	SM	28	6	40 \pm 12	83 \pm 18	125 \pm 19	170 \pm 29	217 \pm 31	257 ^a \pm 29
	M	SI	37	6	39 \pm 10	78 \pm 18	118 \pm 21	159 \pm 28	204 \pm 35	242 ^b \pm 33
	F	SM	28	6	41 \pm 7	81 \pm 14	126 \pm 17	172 \pm 20	224 ^a \pm 27	271 ^a \pm 24
	F	SI	42	6	39 \pm 8	81 \pm 12	123 \pm 16	163 \pm 20	209 ^b \pm 25	248 ^b \pm 28
	M	SM	9	4	73 \pm 13	117 \pm 26	162 \pm 37	199 \pm 45		
	M	SI	292	4	76 \pm 14	116 \pm 21	156 \pm 27	195 \pm 35		
AC	F	SM	12	4	76 \pm 14	119 \pm 18	168 ^a \pm 30	205 \pm 36		
	F	SI	270	4	74 \pm 12	113 \pm 18	152 ^b \pm 26	188 \pm 33		
	M	SM	20	5	75 ^a \pm 11	119 \pm 17	159 \pm 24	197 \pm 34	225 \pm 41	
	M	SI	204	5	79 ^b \pm 11	122 \pm 16	163 \pm 22	203 \pm 28	239 \pm 32	
	F	SM	60	5	80 \pm 15	123 ^a \pm 16	167 ^a \pm 20	209 ^a \pm 22	245 ^a \pm 25	
	F	SI	197	5	78 \pm 11	118 ^b \pm 16	158 ^b \pm 22	195 ^b \pm 30	230 ^b \pm 35	
	M	SM	38	6	79 \pm 10	123 \pm 16	165 \pm 20	207 \pm 25	240 \pm 26	263 \pm 27
	M	SI	75	6	79 \pm 14	119 \pm 16	158 \pm 20	198 \pm 28	233 \pm 34	260 \pm 37
	F	SM	113	6	79 ^a \pm 10	120 ^a \pm 12	162 ^a \pm 18	202 ^a \pm 24	237 ^a \pm 27	263 ^a \pm 28
	F	SI	44	6	74 ^b \pm 14	110 ^b \pm 17	146 ^b \pm 23	178 ^b \pm 31	209 ^b \pm 37	235 ^b \pm 41

size and growth between immature and mature fish were more pronounced among females than among males. These results are in agreement with the findings of Forseth et al. (1994) for the same two species in another Norwegian lake.

To conclude, we found that inter-annual variability in growth and age at maturity of brown trout and Arctic charr in Lake Atnsjøen was partly related to fluctuations in water temperature. However, inter-annual variation in the growth rate of brown trout within Lake Atnsjøen was much lower than among a large number of populations in various regions of Norway. This indicates that life-history characteristics based on a sample from one single occasion can be used in inter-population comparisons, particularly if the information sampled is evaluated with regard to temperature data. It should be noted, however, that Lake Atnsjøen is a relatively large and deep lake, probably representing a relatively stable environment. Thus, in smaller and shallower lakes, and in rivers,

with larger annual fluctuations both in abiotic and biotic factors, life-history characteristics may be more variable and single samples less representative.

Acknowledgements

This study was financially supported by the Directorate for Nature Management (DN) and the Norwegian Council for Scientific and Industrial Research. We thank Arve M. Tvede for providing water temperature data from Lake Atnsjøen, Leidulf Fløystad for ageing the fish and Leif Asbjørn Vøllestad for valuable comments on an earlier draft of the paper.

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A 14-year study of habitat use and diet of brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*) in Lake Atnsjøen, a subalpine Norwegian lake

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Key words: *Salmo trutta*, *Salvelinus alpinus*, abundance, habitat utilisation, diet

Abstract

We studied the spatial and temporal variation in relative abundance (CPUE), habitat use, and diet of Arctic charr (*Salvelinus alpinus* (L.)) and brown trout (*Salmo trutta* L.) in Lake Atnsjøen in southern Norway over a period of 14 years (1985–1998). Fish were sampled with gill nets in epibenthic and pelagic habitats in August each year. Stratified sampling in the epibenthic habitat was carried out with gill net series at three depth zones (0–10, 10–30 and 30–70 m) at one station (1985–1993), and at seven depth zones between 0–3 m and 50–70 m at 10 different stations with multi-mesh gill nets (1994–1998). Lake Atnsjøen is a relatively deep (maximum 80 m), unregulated, subalpine, oligotrophic lake which is not affected to any extent by local or long-range pollution. In shallow epibenthic areas, brown trout is the most abundant species, while Arctic charr dominate deeper epibenthic areas. Epibenthic catches of brown trout at 0–10 m depth were inversely correlated with the catches of Arctic charr. The catches of epibenthic brown trout and Arctic charr did not correlate with mean water temperature in the sampling period. In the pelagic zone, brown trout were mainly caught close to the surface (0–6 m), while Arctic charr were caught between the surface and 12 m depth. Pelagic fish of both species were significantly larger than individuals caught in the epibenthic habitat. The mean size of epibenthic brown trout increased with depth. The opposite trend was evident for Arctic charr, although some larger fish also occupy deeper areas. The size of brown trout in epibenthic areas correlated inversely with CPUE, while no such relationship existed for Arctic charr. The most important food items for Arctic charr in both habitats in August were various species of zooplankton; *Daphnia longispina*, *Bosmina longispina*, *Bythotrephes longimanus* and *Polyphemus pediculus*. Brown trout mainly foraged near the surface on insects in both habitats, but *B. longimanus* and *P. pediculus* were preyed upon to some extent by pelagic specimens. The number of piscivorous individuals was low in both species (1.9–4.5%).

Introduction

Natural ecosystems and communities undergo short and long term variation. Long-time data series are needed to understand this variation, and to enable us to distinguish between natural variation and anthropogenic changes. Many important ecological changes and processes are played out over a long time-scale, and these are often the ones of human relevance (Likens, 1989). Single-year observations of any structure or event from a long-term perspective are of

limited interest as it provides no insight into the long-term behaviour of natural systems (Magnuson, 1990). Long-term investigations are thus required to provide understanding of the mechanisms that regulate the growth and abundance of natural fish populations, and to determine whether changes are due to natural causes or to human activities (Elliott, 1989). Long-term studies are important because we are unable to sense slow changes and we are even more limited in our ability to interpret their causes. Processes that act over decades are hidden and reside in what has been called ‘the in-

visible present' (Magnuson, 1990). In the absence of long-term data series, serious misjudgements may be made in attempts to manage the environment.

Fish communities all over the world are currently affected by anthropogenic influences (Moyle & Leidy, 1992). In Norway, the deposition of acidifying sulphur and nitrogen compounds is regarded as the most serious environmental threat to freshwater ecosystems including fish communities (Hesthagen et al., 1999), causing for example rapid changes in age structure, decreasing population abundance, and finally extinction (Schindler et al., 1991). Freshwater habitats are also impacted by eutrophication, physical destruction, water withdrawal, toxic chemical pollution, introduction of alien species, and overfishing.

In Norwegian freshwaters, brown trout (*Salmo trutta* L.) and Arctic charr (*Salvelinus alpinus* (L.)) are the two dominant fish species, and they commonly occur in sympatry (Hesthagen et al., 1999). Natural changes over time in the interaction between Arctic charr and brown trout may be caused by variable recruitment and variation in the abundance of various prey types. Utilisation of limited resources causes exploitative and interference competition (Nilsson, 1960, 1963, 1965), but differences in resource utilisation may also be due to selective differences (Langeland et al., 1991). Brown trout live mainly in littoral and near-surface waters in both sympatric and allopatric populations (Dahl, 1917; Ball & Jones, 1962; Thorpe, 1974; Svärdsen, 1976; Langeland et al., 1991). Arctic charr, on the other hand, exploit littoral areas in allopatry, while they tend to be more confined to deep epibenthic and pelagic areas in sympatry with brown trout (Nilsson, 1965; Langeland et al., 1991; Langeland & L'Abée-Lund, 1998). However, the habitat and diet choice usually change with body size. Among large fish, which are not vulnerable to predation, the choice of habitat should be determined by prey availability and energy spent on searching for, capturing and dealing with prey (Werner & Hall, 1974; Abrahams & Dill, 1989). Young and small fish often occupy low-risk habitats compared with older, larger individuals (Jonsson & Gravem, 1985; Jonsson, 1989; Sandlund et al., 1992; Hesthagen et al., 1995). Body size is also an important factor in intraspecific habitat use by sympatric brown trout and Arctic charr, as smaller fish appear to be competitively inferior to larger conspecifics (Hindar & Jonsson, 1982; Jonsson & Gravem, 1985; Hegge et al., 1989). Fish size may also be inversely related to abundance (Hesthagen & Johnsen, 1992), and it has been shown that different

size groups of fish segregate by depth (Hegge et al., 1989; L'Abée-Lund et al., 1993).

In this paper we present a 14-year study of the spatial and temporal variation in abundance, and use of space and food, of Arctic charr and brown trout in Lake Atnsjøen, a relatively pristine subalpine lake in southeastern Norway.

Study area

Lake Atnsjøen (61° 51' N, 10° 13' E) is located 701 m a.s.l. in the Atna River (Fig. 1). The unregulated Atna catchment is part of the Glomma watershed, and covers an area of 1323 km². It originates in the Rondane Mountains at altitudes of 1400–1500 m a.s.l. Lake Atnsjøen is an oligotrophic lake with a surface area of 4.8 km², and with mean and maximum depths of 35 m and 80 m respectively (Hegge et al., 1989). The concentration of calcium usually ranges between 0.5–1.2 mg l⁻¹, and pH varies between 6.0–6.5 (Blakar et al., 1997). Secchi disk depth is normally about 9–10 m (Halvorsen et al., 2003). The bottom profile of the lake is steep, resulting in a narrow littoral zone with depths of 10–11 m about 10 m from the shore line (Austigard & Holmedal, 1998). The bottom is covered with stones and gravel at depths of 0–5 m, with a dense vegetation of *Isoetes lacustris* L. between 5–10 m, and fine material in deeper areas. Average water temperatures in Lake Atnsjøen in July and August usually range between 10.0 and 14.0°C (Tvede, 2003). In addition to Arctic charr and brown trout, Lake Atnsjøen supports Siberian sculpin (*Cottus poecilopus* (Heckel)) and a very sparse population of European minnow (*Phoxinus phoxinus* (L.)) (Hesthagen & Sandlund, 2004).

Material and methods

Test-fishing was carried out with epibenthic and pelagic nets between 4–21 August each year from 1985 to 1998. During the first nine years of the study (1985–1993), sampling was carried out at one epibenthic station (E2) and one pelagic station (P1) (Fig. 1). During this part of the study we used epibenthic (1.5 m deep and 25 m long) and pelagic nets (6 m deep and 25 m long) with eight different mesh sizes between 16–45 mm (knot to knot), constituting one series (cf. Jensen, 1977). The epibenthic nets were set at three depth intervals: 0–10, 10–30 and 30–70 m. In the

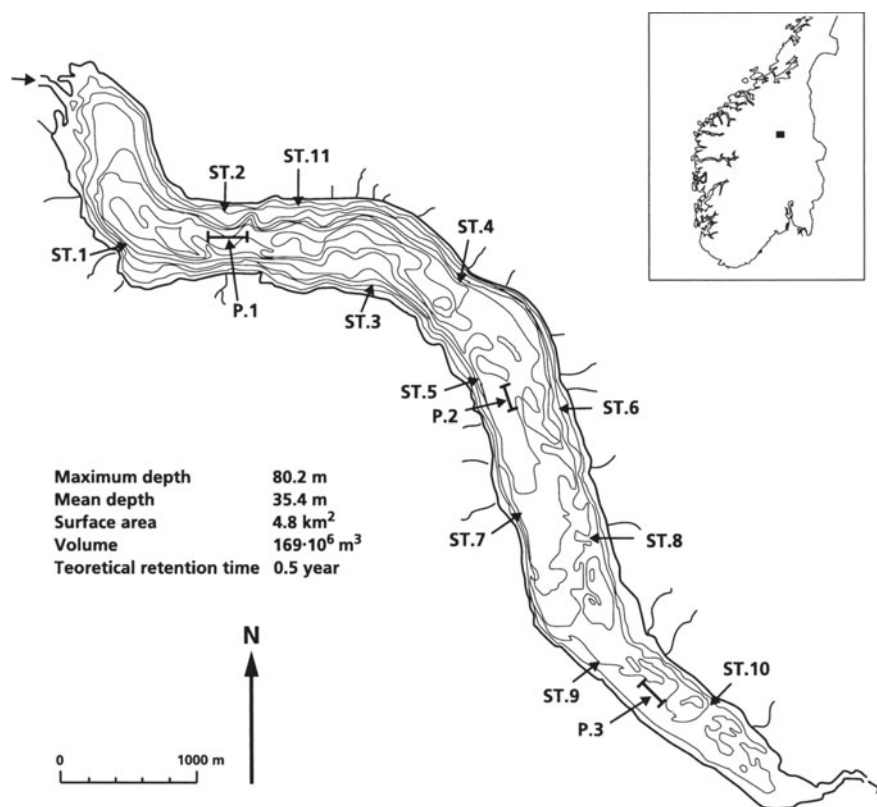


Figure 1. Lake Atnsjøen with indicated positions of the sampling stations used for gill netting in the epibenthic habitat (E1-E11) and pelagic habitat (P1-P3).

shallow waters (0–10 m), the nets were set singly from the shoreline, with a distance of about 50 meters between each net, totally one series. At intermediate depths (10–30 m), four gill nets were tied together in one chain, and set with a distance of about 100 m between each chain. These nets were set in two following nights with different mesh size sequences, totally 2 series. In the deepest area (30–70 m), eight nets were tied together in one chain. Pelagic gill nets were set at two depths; 0–6 m and 6–12 m, with one series in each depth interval.

From 1994 to 1998, we used multi-mesh survey nets in both epibenthic and pelagic habitats. The epibenthic nets are 30 m long and 1.5 m deep and consist of 12 mesh sizes between 5–55 mm (knot to knot), i.e. panels of 2.5 m of each mesh size (Appelberg et al., 1995). These nets were set at 10 different stations throughout the lake (Fig. 1), and at 4–7 depth intervals depending on the actual depths at each station: 0–3 m, 3–6 m, 6–12 m, 12–20 m, 20–35 m, 35–50 m and 50–70 m; a total of 56 nets. The pelagic nets were 54 m long and 6 m deep and consisted of eight mesh sizes

between 10–45 mm, i. e. panels of 6.75 m of each mesh size. These nets were set over the deepest area of the lake at depths of 0–6 m and 6–12 m at three stations (Fig. 1). The depths of fish retained in pelagic nets were measured to the nearest metre.

The nets were set in the evening, and lifted the following morning. The catch per unit effort (CPUE) is presented as number of fish per 100 m² net area per 12 hours fishing. In order to compare the epibenthic catches throughout the study period (1985–1998), only catches in net panels with mesh sizes between 16–45 mm at station E2 in 1994–1998 were included.

Data on total length (L, mm), weight (W, g) and degree of sexual maturity were obtained from each fish. For both Arctic charr and brown trout caught in pelagic and epibenthic habitats, the contents of about 20 stomachs were analysed each year. Individual prey items were counted and the body length of intact individuals was measured using a stereoscopic microscope. The biomass of the stomach content was determined as dry weight, based on the regression

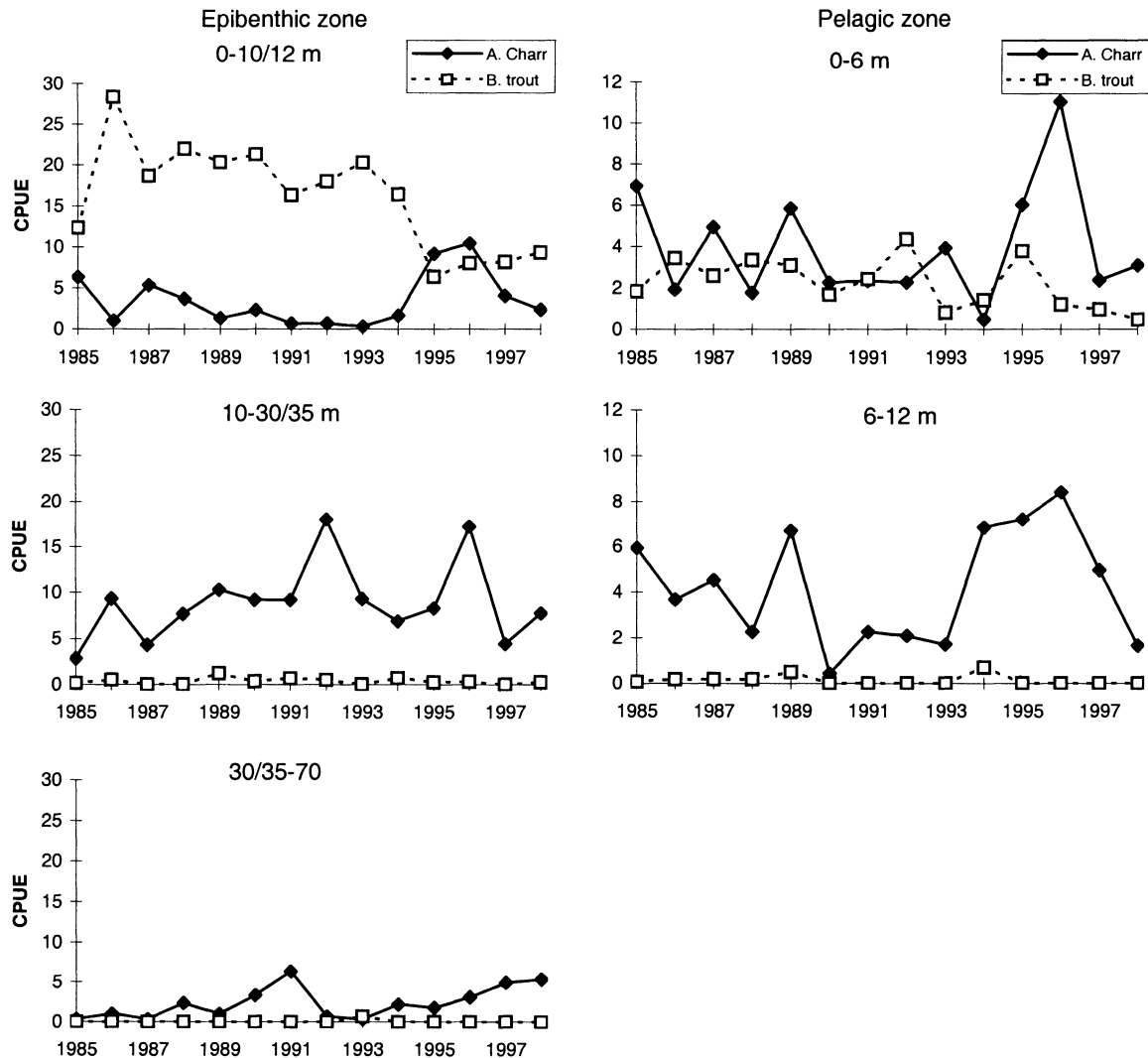


Figure 2. Catch per 100 m² net area per 12 h fishing (CPUE) for Arctic charr and brown trout in the epibenthic habitat (0–12, 12–35 and 35–70 m depth) and pelagic habitat (0–6 and 6–12 m depth) in Lake Atnsjøen, 1985–1998.

between body length, or width of the head, and weight (Breistein & Nøst, 1997). The diets of both fish species are presented as percent dry weight of each food category. From 1994 to 1998, stomachs were sampled from the first 25 specimens that were caught in each habitat, and not necessarily from the same stations.

Results

In the epibenthic habitat, brown trout dominated in the littoral zone (0–12 m depth), while Arctic charr were most abundant in deeper waters (12–70 m depth) (Fig. 2). However, from 1993 to 1996 CPUE of Arctic

charr increased in the littoral zone, with a corresponding reduction in brown trout catches. The CPUE of Arctic charr at 10–35 m depth appeared to be increasing during the study period, while catches of brown trout remained stable at this depth (Fig. 2). Brown trout were rarely caught in the deep profundal zone (35–70 m depth). CPUE of Arctic charr at this depth was usually low, but showed moderate maxima in 1991 and 1998. Mean CPUE \pm SD of epibenthic Arctic charr and brown trout during the study period were 17.7 ± 8.5 and 18.7 ± 4.9 respectively. Total catches of Arctic charr reached a maximum in 1996 in both habitats.

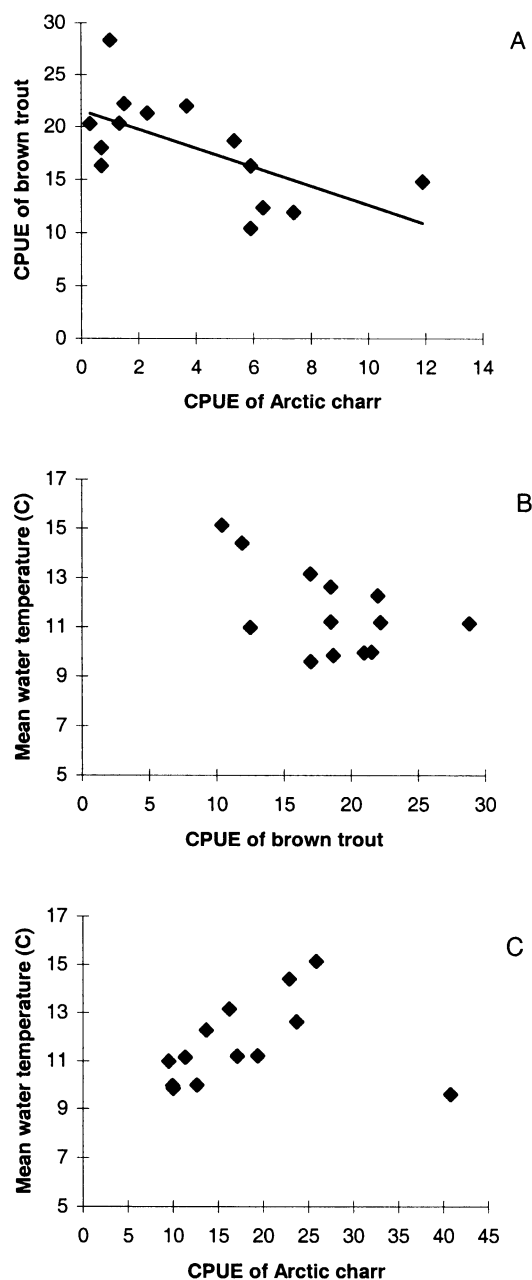


Figure 3. Linear regression ($y = -0.90x + 21.55$, $R^2 = 0.39$, $p < 0.05$) between CPUE for epibenthic brown trout and Arctic charr at 0–12 m depth (A), and between mean water temperature and CPUE for brown trout (B, $p > 0.05$) and Arctic charr (C, $p > 0.05$) in the epibenthic habitat in Lake Atnsjøen, 1985–1998.

Catches of epibenthic Arctic charr and brown trout were inversely related (Fig. 3). There was no correlation between the total catch (all depths included) of the two fish species. There was a tendency towards higher catches of brown trout (all depths included) with de-

Table 1. Numbers of Arctic charr and brown trout caught with gill nets in epibenthic and pelagic habitats of Lake Atnsjøen, 1985–1998.

Year	Arctic charr		Brown trout	
	Epibenthic	Pelagic	Epibenthic	Pelagic
1985	37	154	38	23
1986	62	67	88	43
1987	43	113	56	33
1988	64	48	66	42
1989	68	150	68	43
1990	72	32	66	20
1991	76	55	53	29
1992	112	52	57	52
1993	57	68	64	9
1994	129	65	157	19
1995	193	116	61	32
1996	301	144	70	10
1997	146	63	84	8
1998	126	40	79	4

creasing water temperature during the sampling period (Fig. 3, linear regression, $p = 0.064$), while CPUE of Arctic charr and mean water temperature showed no correlation ($p = 0.48$). However, when the data from 1996 were removed, the correlation for Arctic charr was highly significant ($y = 2.77x - 16.75$, $R^2 = 0.68$, $p < 0.001$). There was no correlation between mean water temperature and CPUE of brown trout and Arctic charr in different depth zones in the epibenthic habitat ($p > 0.05$).

Arctic charr were considerably more abundant than brown trout in the pelagic habitat (Table 1, Fig. 2). There were large temporal and spatial variations in the abundance of pelagic fish. Most pelagic brown trout were caught at depths between 0–6 m, while Arctic charr were more evenly distributed between 0–6 m and 6–12 m depths (Fig. 2). Differences between the two species in CPUE were less pronounced in the upper depth zone (0–6 m), and in five periods brown trout was more abundant than Arctic charr in this depth zone. There was no significant correlation between the CPUE of pelagic brown trout and Arctic charr or between mean water temperature and catches of pelagic fish (linear regressions, $p > 0.05$).

There was considerable horizontal and temporal variation in the epibenthic catches of both brown trout and Arctic charr (Fig. 4). In general, catches of Arctic charr were larger on the eastern than the western side of the lake (Figs 1 and 4). On the other hand, brown

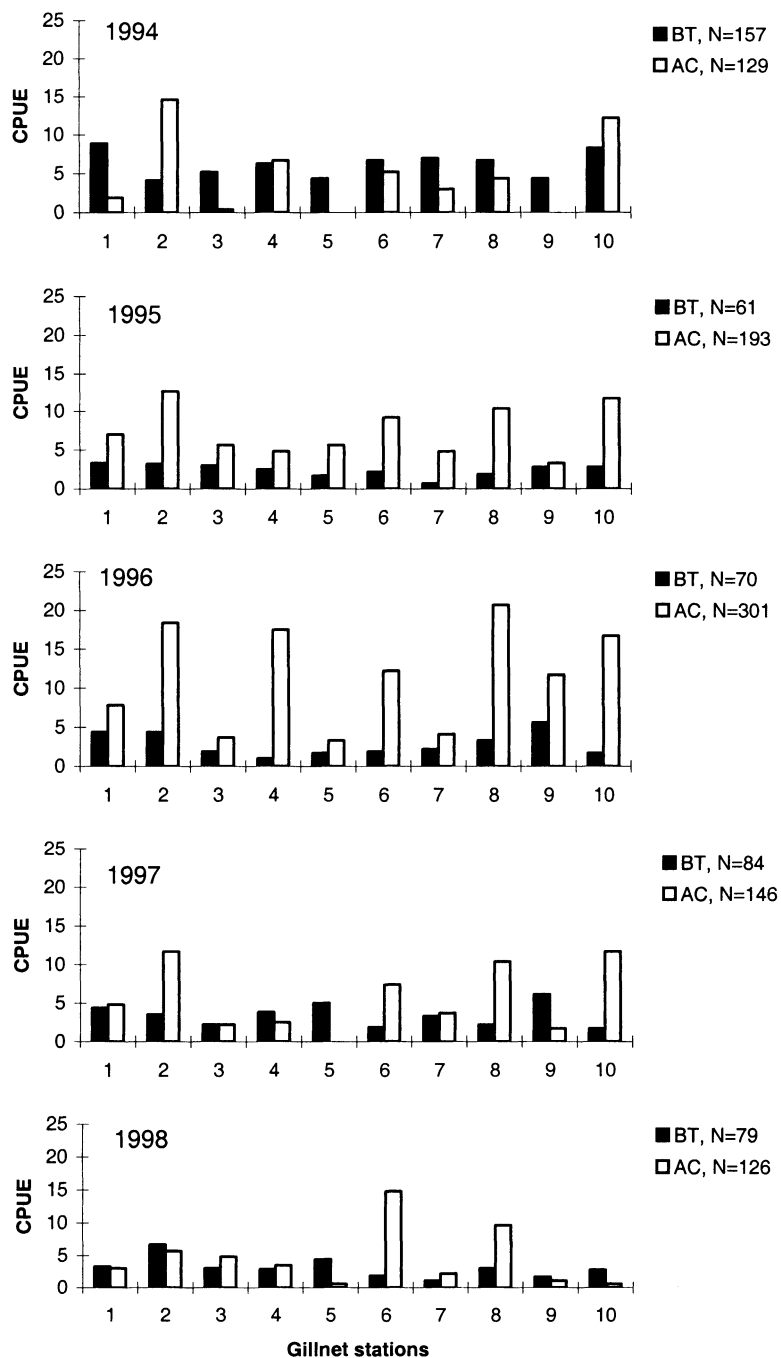


Figure 4. Spatial and temporal variation in the abundance (CPUE) of Arctic charr (AC) and brown trout (BT) based on catches in multi-mesh gill nets at 10 different stations in the epibenthic habitat in Lake Atnsjøen, 1994–1998. N = number of fish.

trout were more evenly distributed throughout the lake and exhibited less annual variation. In 1995 and 1996, Arctic charr were more abundant than brown trout at all stations.

Pelagic brown trout and Arctic charr were significantly larger than conspecifics caught in the epibenthic habitat (Kolmogorov–Smirnov two-sample test, $p < 0.05$). Most pelagic individuals of both species were between 25–30 cm in total length, as opposed to 15–20 cm among epibenthic fish. Furthermore, the body size of epibenthic Arctic charr decreased with increasing depth, except that some larger individuals of Arctic charr also occupy areas deeper than 35 m (Fig. 5). The body size of epibenthic brown trout increased with increasing depth. There was no significant relationship between the mean length of fish and their vertical distribution in the pelagic habitat ($p > 0.05$). However, in 1994 brown trout was caught at all depths while Arctic charr were absent from the surface area (0–3 m), and segregation in size of Arctic charr by depth was more evident compared to the other periods (1995–1998).

During 1994–1998, there was a significant decrease in the size of brown trout with increasing CPUE in the two shallowest epibenthic zones; 0–3 and 3–6 m (linear regression, $p < 0.05$), and a similar trend at 6–12 m depth (Fig. 6, $p = 0.06$). No such relationship was found for Arctic charr in any of the three depth zones tested; 6–12, 12–20 and 20–35 m ($p > 0.05$).

Various zooplankton species were the most important food items for Arctic charr in both habitats in August (Fig. 7). In the epibenthic habitat, *Daphnia longispina* and *Bosmina longispina* were the dominant prey items. *Holopedium gibberum* was also important food for Arctic charr in both habitats in 1995 and 1996. *Bythotrephes longimanus*, and in certain years, *Polyphemus pediculus*, dominated the diet of pelagic fish. Brown trout in both habitats mostly foraged near the surface on insects (Fig. 8). Zooplankton contributed very little to the diet of brown trout, except that *B. longimanus* and *P. pediculus* to some extent was taken by pelagic individuals in some years. In 1995, *B. longimanus* represented almost 50% (dry weight) of the diet of pelagic brown trout. More pelagic brown trout had also eaten *B. longispina* and *D. longispina* in that year than in other years. *P. pediculus* was found in stomachs of Arctic charr and brown trout until 1989, but rarely in later years. Throughout the study, 4.5% ($n = 16$) of the examined brown trout >21 cm in total length had consumed fish. Most of the piscivorous specimens ($n = 11$) were caught at depths between

0–12 m in the epibenthic habitat. Only seven individuals (1.9%) of Arctic charr >24 cm in total length had fish in their stomachs. Most prey fish were unidentified, though Siberian sculpin and Arctic charr were recorded in the stomachs of brown trout, whereas only Siberian sculpin were identified in the stomachs of Arctic charr.

Discussion

Long-term trends in fish abundance have been related to overfishing, changes in the habitat, invasion by other fish species and climatic variability (Evans, 1992). However, in Lake Atnsjøen the variation in abundance of brown trout and Arctic charr cannot be related to any of these factors.

Brown trout mainly occupied the littoral zone, while Arctic charr were most abundant at depths between 12–35 m. Competition between different species of fish occurs when they utilise common limited resources (Werner & Hall, 1976; Werner et al., 1983). Epibenthic areas in lakes are usually a low-risk habitat if sufficient access to cover and hiding places is available. In Lake Atnsjøen, depths between 0–5 m are a more rewarding zone, due to both more shelter and more abundant food (Aagaard et al., 1997). The lake has a steep shore line, and the area of the littoral zone is therefore quite restricted. Catches of brown trout and Arctic charr in the littoral zone were inversely correlated, indicating a possible competitive interaction between them. Arctic charr move into the more productive and warmer area of the epibenthic when densities of brown trout are low. There was a non-significant tendency for catches of brown trout to decrease with increasing water temperature, while catches of Arctic charr tended to increase as temperatures increased. Field studies has indicated that Arctic charr avoid waters warmer than 16 °C in both epibenthic and pelagic habitats (Langeland & L'Abée-Lund, 1998), but as mean temperatures in Lake Atnsjøen did not exceed 15 °C during the study period, temperature may not be an important factor here. Our results do not, however, support previous studies indicating that Arctic charr are more active than brown trout at low temperatures (Filipsson & Svärdson, 1976).

In 1995, there was a large flood in the Atna watercourse, reaching a level that occurs only at intervals of 100–200 years (Erichsen, 1995). The flood caused a decrease in water transparency (i.e. Secchi

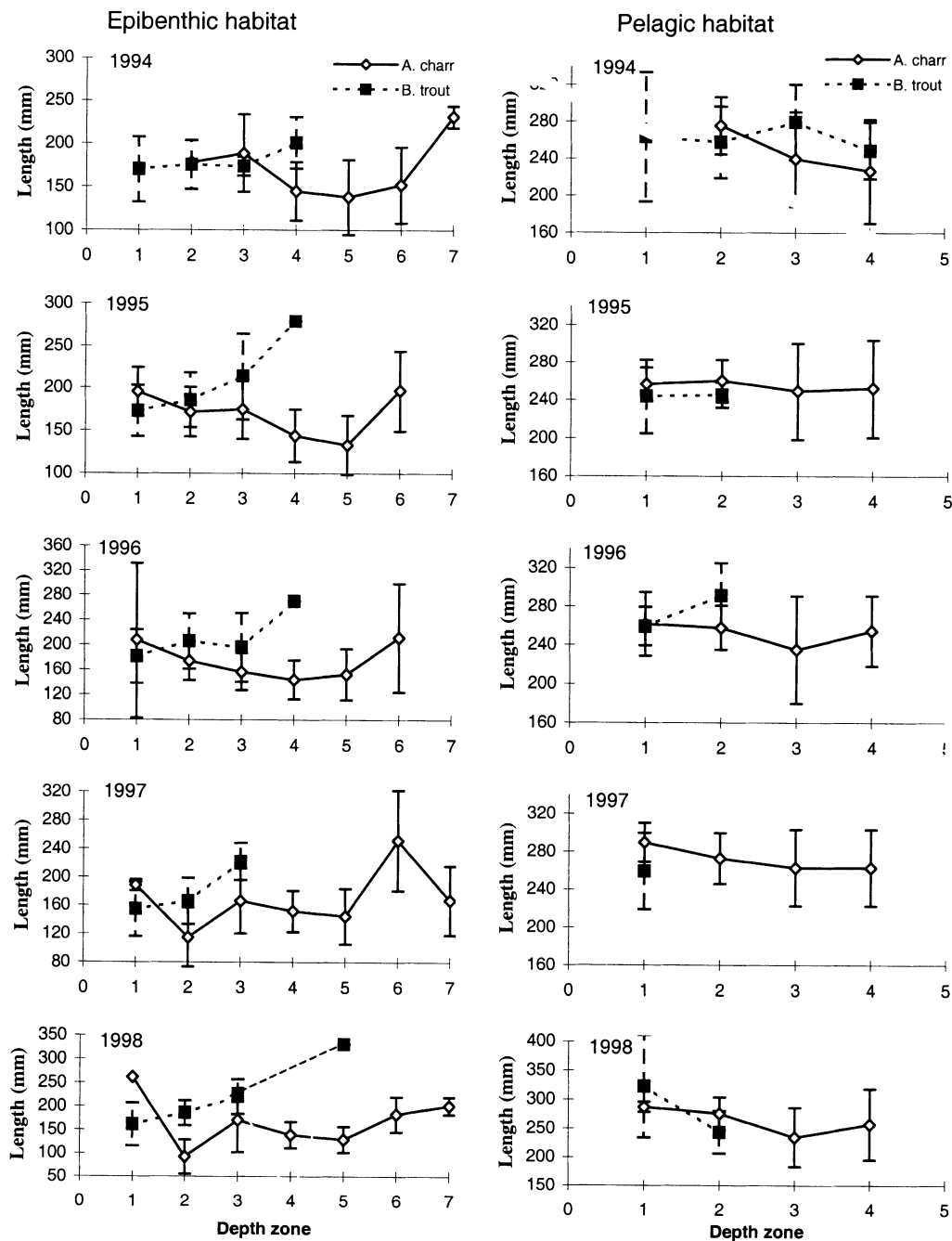


Figure 5. Mean length \pm standard deviation of Arctic charr and brown trout caught at different depths in epibenthic and pelagic habitats in Lake Atnsjøen, 1994–1998. The different depths in the epibenthic habitat was: 1 = 0–3 m, 2 = 3–6 m, 3 = 6–12 m, 4 = 12–20 m, 5 = 20–35 m, 6 = 35–50 m and 7 = 50–70 m, and in the pelagic habitat: 1 = 0–3 m, 2 = 3–6 m, 3 = 6–9 m and 4 = 9–12 m.

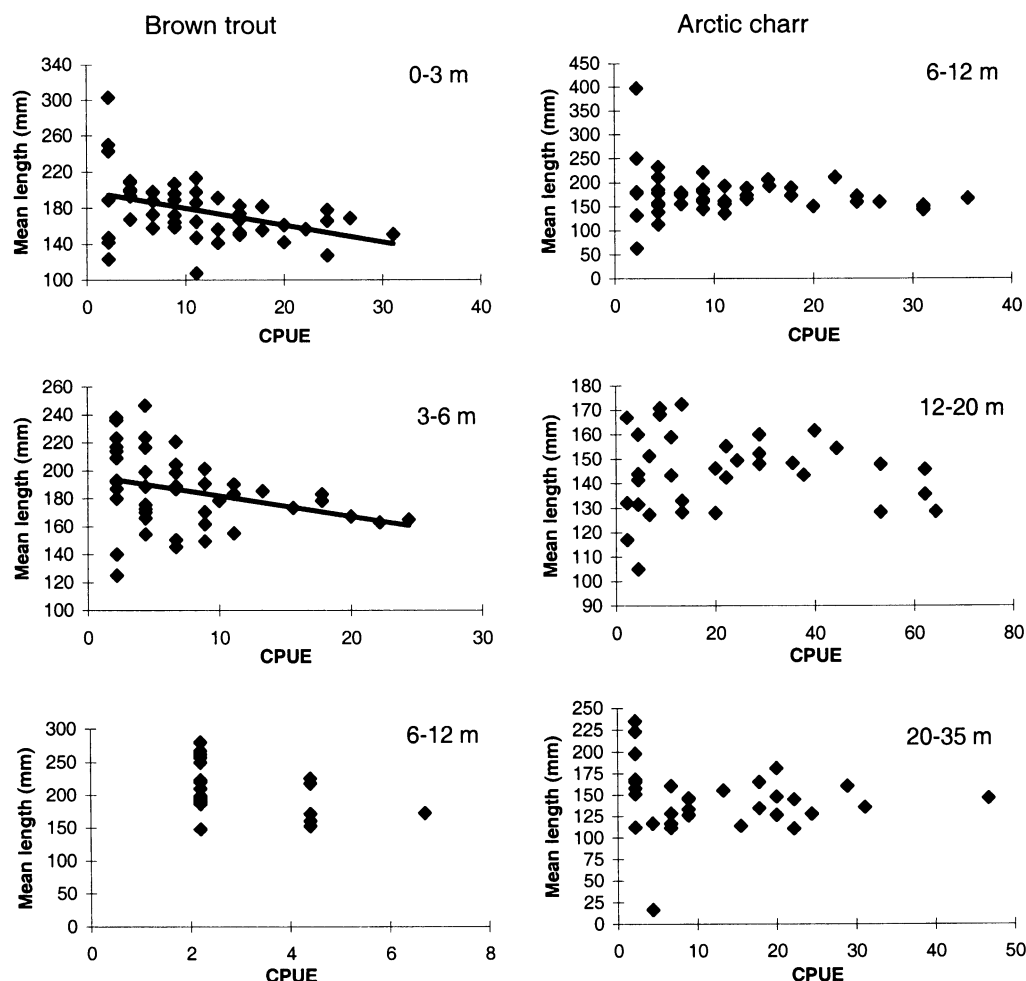


Figure 6. Mean length in relation to the abundance (CPUE) of brown trout and Arctic charr at different depth zones in the epibenthic habitat of Lake Atnsjøen, 1994–1998. Linear regression for brown trout at depths between 0–3 m (number of observations = 50): $y = -1.87x + 198.31$, $R^2 = 0.1705$, 3–6 m (number of observations = 45): $y = -1.47x + 196.71$, $R^2 = 0.0975$.

depth) from 9–10 m to 3.5 m and provided the lake with large amounts of organic and inorganic material (Halvorsen et al. 2004; Austigard & Holmedal, 1998). Large catches of Arctic charr in 1995 and 1996 may have been an indirect effect of this flood due to increased densities of zooplankton (Halvorsen et al. 2004). This is contrary to the observations of Patalas & Salki (1984) who documented reduced abundance of crustacean zooplankton with increases in turbidity and suspended sediment. However, the flood in Lake Atnsjøen in 1995 merely resulted in short term fall in water transparency, as Secchi depth was measured at 10 m already two months after the flood (Austigard & Holmedal, 1998).

Interactions between the two salmonid species were less pronounced in the pelagic zone of Lake

Atnsjøen. There was no correlation between temperature and catches of brown trout and Arctic charr in this habitat, or between the CPUE of the two fish species. Hence, the large spatial and temporal variations in the two species' use of the pelagic habitat must be due to other factors. Catches of pelagic Arctic charr were significantly correlated with the density of zooplankton, while there was no such correlation for brown trout (Saksgård, unpubl.) Because these two species feed on different food items, and the difference between CPUE in the upper strata of the pelagic habitat was small compared to the epibenthic habitat, there appears to be no competition in the pelagic zone. However, in 1994, brown trout were caught at all depths between 0–12 m, and segregation in size of Arctic charr by depth was also highly evident. Arctic charr and brown

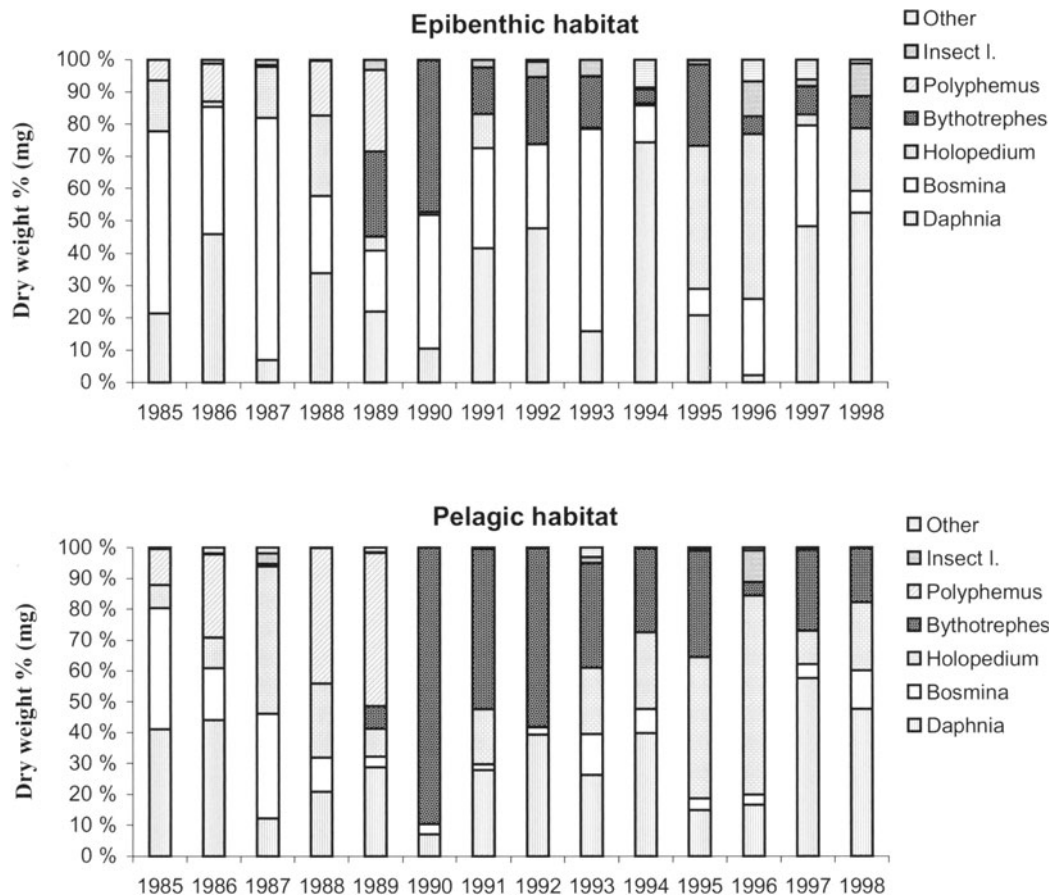


Figure 7. Diet of Arctic charr expressed as percent composition of dry weight in the epibenthic and pelagic habitats in Lake Atnsjøen, 1985–1998. Figures at the top of each column indicate the number of stomachs analysed.

trout differ in many aspects of their ecology, and higher aggressiveness in brown trout is one of them (Nilsson, 1963; Jobling & Reinsnes, 1986). Large brown trout often chase smaller individuals (Haraldstad & Jonsson, 1983). Spatial segregation in depth between the two species in the epibenthic habitat may be due to interference competition, as brown trout are more aggressive. In the pelagic habitat, on the other hand, segregation in depth according to size is probably due to predator avoidance, since small fish are more vulnerable to predation than larger ones.

Smaller Arctic charr and brown trout were mainly caught in the epibenthic habitat, while larger conspecifics (>20 cm) occupied the pelagic habitat. Predation risk is a major factor in determining the habitat choice of smaller fish, but as they grow in size, predation risk decreases (Crowder & Cooper, 1982; Werner et al., 1983). Body size has been shown to be an important determinant of habitat use by both sympatric

and allopatric brown trout and Arctic charr (Hindar & Jonsson, 1982; Jonsson & Gravem, 1985; Hegge et al., 1989). In the epibenthic zone of Lake Atnsjøen, small brown trout stayed close to the shore line, while larger individuals occupied deeper areas. This is in agreement with Persson's (1985) hypothesis that smaller animals tend to be superior in exploitative competition. Furthermore, epibenthic brown trout were largest in areas with lower fish density, probably as a result of intraspecific competition for food and space. However, there was no such relationship between abundance and size of Arctic charr, as larger individuals were caught in shallow areas together with smaller brown trout, as well as in the deepest part of the epibenthic habitat. It has been shown that larger Arctic charr moved into the profundal zone following the removal of large numbers of smaller individuals (Klemetsen & Dahl-Hansen, 1995). These authors indicated that this was an effect of increased cannibalism and that

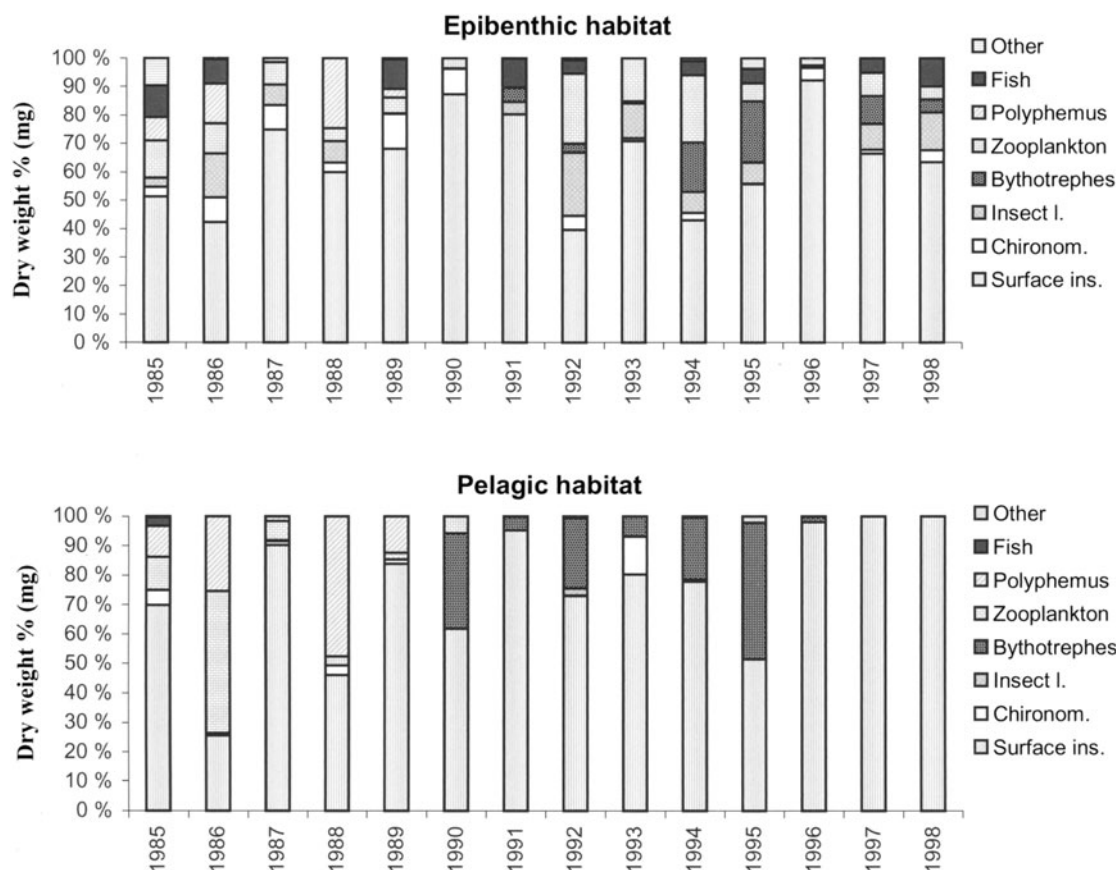


Figure 8. Diet of brown trout expressed as percentage composition of dry weight in the epibenthic and pelagic habitats in Lake Atnsjøen, 1985–1998. Figures at the top of each column indicate the number of stomachs analysed.

larger Arctic charr searched in all habitats for smaller prey fish. In Lake Atnsjøen, cannibalistic Arctic charr seem to be rare, as less than 2% of sampled fish had fish in their stomachs. Smaller epibenthic Arctic charr in Lake Atnsjøen stayed in the same depth as larger brown trout, i.e. at depths between 12–20 m. The risk of predation for Arctic charr is probably lower in this zone, due to low light intensities. Only a small fraction of brown trout had eaten fish (4.5%).

In Lake Atnsjøen, Siberian sculpin also compete with the two salmonid species for space and food in the littoral zone (Austigard & Holmedal, 1998). In August, Siberian sculpin tend to occupy depths of 5–10 m, which is the intermediate zone between brown trout and Arctic charr. It has previously been shown that brown trout may prey on sculpin (Newman & Waters, 1984; Hanson et al., 1992). Thus, the habitat use of Siberian sculpin may reflect an attempt to avoid predation by larger brown trout and Arctic charr. In Lake Atnsjøen it seems likely that Siberian sculpin and

small individuals of Arctic charr and brown trout experience a trade-off between access to food and hiding from predators (cf. Mittelbach, 1981; Fraser & Cerri, 1982; Werner et al., 1983; Wotton, 1990).

The choice of food items of the fish species in a community appears to be related to their spatial distribution. In our study, choice of food items by Arctic charr and brown trout differed in both the epibenthic and pelagic habitats. In epibenthic areas, differences in diet may partly be explained by horizontal segregation because at the depths occupied by Arctic charr, zooplankton is the most available food item. In 1995, an exceptionally high number of pelagic brown trout had eaten various zooplankton species. *B. longimanus* was one of the most important food items for both fish species in this period. A study throughout the ice-free season in 1995 showed the largest diet overlap between epibenthic Arctic charr and Siberian sculpins in August (Austigard & Holmedal, 1998). This was because both species preyed heavily on *B. longispina*,

which was present at high densities during this period (Halvorsen et al., 2003). Niche theory predicts that individuals should specialise on different prey types when competition is strong (Putman, 1994). Due to the high density of zooplankton in Lake Atnsjøen in 1995, competition between the different fish species seems to have been less harsh in that year, as their diet was more similar.

In the epibenthic habitat, catches of Arctic charr were largest on the east side of the lake in 1994–1998. Densities of zooplankton have also been shown to be highest in this area, probably due to the patterns of currents in the lake (Halvorsen & Papinska, 1997). The larger catches of Arctic charr on the east side of the lake might therefore be due to higher zooplankton densities. Thus, for comparison of the diet from one year to another, fish should be collected from the same area of the lake.

Our study demonstrated large spatial and temporal variations in abundance and the use of space and food of Arctic charr and brown trout in Lake Atnsjøen. This suggests that long-term monitoring studies are needed to establish baseline values for characterising their relative abundances and natural variation in resource utilisation. We conclude that the abundance of Arctic charr in the littoral zone is dependent on the density of brown trout. Our results suggest that catches of epibenthic Arctic charr are positively correlated to water temperature under the prevailing temperatures in this mountain lake. Arctic charr seem to avoid temperatures above 16 °C (Langeland & L'Abée-Lund, 1998), but the mean temperature during our study never exceeded that value. Thus, a change in the climate due to for example global warming, might have a significant effect on the relative abundance of brown trout and Arctic charr in a temperate lake. In the pelagic habitat, densities of zooplankton seem to be the main factor determining the relative abundance of Arctic charr. Catches of brown trout were generally low in the pelagic habitat. Epibenthic areas are more nutritionally profitable, particularly in oligotrophic mountain lakes, where zooplankton density is very low (Halvorsen & Papinska, 1997). Variable year class strength may also influence the abundance of fish in the lake. Brown trout spawn in rivers and streams, whereas Arctic charr spawn in the lake. In this mountain system, we might expect abiotic conditions to be more variable in the streams than in the lake. Thus, the recruitment of brown trout may be more impacted by climatic factors.

Acknowledgements

Thanks are due to Ola Hegge and Jostein Skurdal for initiating this study; Ola Hegge was also in charge of the fish sampling from 1985–1993. We thank Leidulf Fløystad and Helen Guldseth at NINA for participating in the test-fishing in recent years, and Odd Terje Sandlund for valuable comments on the manuscript. The study was financed by the Directorate for Nature Management (DN) and the Norwegian Council for Scientific and Industrial Research.

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PERSPECTIVE



Long term monitoring and research in an alpine–boreal watershed: Atnadalen in perspective

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Watershed management

It is becoming increasingly evident that the watershed is an appropriate scale for improved understanding of the dynamic processes in rivers and lakes (cf. Boon et al., 2000; Biswas & Tortajada, 2001). During recent years, this approach has for example been adopted in modern management tools such as the Water Framework Directive (WFD) of the European Union (EU, 2000), and in international environmental assessment exercises such as the Millennium Ecosystem Assessment (www.millenniumassessment.org; DN, 2002). The ‘ecosystem approach’ adopted by the Convention on Biological Diversity is also promoting a holistic watershed approach in biodiversity and resources management (Schei et al., 1999; www.biodiv.org). Consequently, management oriented research has to focus on watershed processes in order to provide the required information that needs to underpin future management.

Watershed management is a complex issue, requiring information on a diversity of variables, including both terrestrial and aquatic ecosystem components (Ward, 1998). The complexity of the issues is enhanced by the interaction between terrestrial and aquatic elements, and the spatial and temporal dynamics of physical and chemical conditions, ecological processes, food webs, and populations. In addition, social sciences must provide insights into the economic, social and cultural factors of the human society (cf. e.g. Østdahl et al., 2002). Even when restricting ourselves to the natural sciences, we need to grasp the level of natural variation in a great number of variables, and the major interactions between the variables, if we are to satisfy the needs identified for example in the WFD.

This essay summarizes the information on the Atna watercourse reported in this volume, and attempts to evaluate the usefulness of the various parameters recorded during the FORSKREF programme. The parameters or data sets are evaluated with a view to their usefulness in relation to (1) monitoring of environmental conditions, (2) description of reference conditions in an alpine – boreal water course, and (3) characterization of surface water body types and reference sites (cf. the WFD).

The concept ‘usefulness’ incorporates at least two important aspects, related to a cost-benefit consideration. Firstly, the parameter has to relate to the ecosystem condition, i.e. it has to contain an element of indicator. Secondly, the efforts required to collect data has to be reasonable in terms of time, effort, equipment, and staff qualifications. Included in this are also the efforts needed to analyse data, in terms of time and complexity.

The Water Framework Directive (WFD) – different data needs

A central element of the WFD is the need to determine the ecological status of surface water bodies, based mainly on information regarding aquatic flora (including phytoplankton and periphyton), aquatic macroinvertebrates, and fish. The Directive calls for a network of sites illustrating the reference condition for each water type. The reference condition for each type of surface water site should be established based on biological parameters as well as physical-chemical and hydro-morphological conditions. The investigations in the Atna watercourse have included documentation over a number of years of the biological components required in the WFD context as well as a number of

physio-chemical and hydromorphological parameters. Thus, the data time series from Atna may be of general value as they demonstrate the natural variation in a reference condition alpine/sub-alpine water course. With the amount of data for the Atna watershed presented in this volume, and the continued collection of data (Lindstrøm et al., 2002), Atna may be a good candidate as an illustration site in the WFD context.

Reference localities are also required in national monitoring programmes. In particular, understanding the impacts of climate change on watersheds and aquatic life requires long term monitoring data on a number of parameters (SFT, 1992; Sygna & Brien, 2001; NRC, 2001). With the basis created by the data reported here, Atna is also a valuable locality in relation to understanding long term processes in erosion and sedimentation in pristine watersheds (Bogen & Bønsnes, 1999).

Monitoring aspects

It is well known that natural variation in ecosystem parameters may be great even in pristine environments (cf. Pimm, 1991). This has to be accounted for when determining the ecological status of any ecosystem. The background of natural variation over time is also important in the design of environmental monitoring programmes, as it is crucial to distinguish between natural and anthropogenic variation.

There is a general lack of good time series of ecological data. In particular, data from simultaneous sampling of many parameters over significant space and time has been rare. Thus, the initiation of the FORSKREF programme in 1985 was quite visionary in relation to present day needs (Tvede & Halvorsen, 2004). The subsequent follow up over a 15-year period has produced a unique set of data on an alpine–boreal water course at approximately 62° N 10° E in north-western Europe. These data are of high relevance to the WFD as well as other management strategies and monitoring programmes.

Parameters

The FORSKREF data reported in this volume includes information on a number of physical and chemical parameters, such as climate, hydrology, sediment transport, and water chemistry. In addition, data are reported for phytoplankton and zooplankton (in Lake

Atnasjøen) and periphyton and benthic invertebrates (in lotic habitats). Finally, comprehensive data on the fish communities and the major fish species in both lotic and limnic habitats are also reported. Most of the data series cover a number of years. Consequently, they form a comprehensive picture of the normal situation and the natural spatial and temporal variation in an alpine–boreal watercourse.

Spatial variation

The river continuum concept (Vannote et al., 1980) realises the fact that there are interactions on a spatial scale along the water course, with processes upstream influencing events downstream, and migration of fish and other organisms transporting energy and organic matter upstream. The flood pulse concept (Junk et al., 1989) emphasises the interrelatedness between the watercourse and its adjoining land. Both concepts stress the spatial aspects of watershed dynamics. In addition, the temporal dynamics in watersheds are essential, both at the seasonal and annual basis. Because most research programs are severely restricted in time, very little is known about the long term dynamics of water courses, and its various biological components. In order to understand the restrictions and possible value of data from short term (commonly one to three years) research projects, it is essential to know, for example, the normal medium to long term year to year variation in biological parameters.

The Atna watershed stretches from the alpine to the boreal region, while a major part of the area lies within the birch belt (also called the sub-alpine) zone. The total altitude gradient is from 2160 to 338 m a.s.l. More than 60% of the catchment area is between 700 and 1100 m altitude, i.e. above the treeline.

The altitudinal gradient is reflected in pronounced spatial gradients in all physical, chemical and biological parameters. The climate in the Atna watershed is of a continental type, characterised by precipitation minimum in late winter and maximum in summer. Annual precipitation at 700 m altitude is approx. 500 mm, while precipitation in the alpine areas at higher altitudes is significantly higher (Nordli & Grimenes, 2004). The one major lake in the watershed, Lake Atnsjøen (701 m a.s.l.), with a surface area of 4.8 km², constitutes approx. 1% of the total watershed and has a quite pronounced effect on the local climate as well as the ecological conditions in the water course (Halvorsen, 2004; Tvede, 2004; Nordli & Grimenes,

2004). The geology of the watershed is characterised by nutrient poor quartzite. The Quarternary sedimentary deposits are also nutrient poor. Consequently the waters of the rivers and lakes are low in dissolved solids (Bogen, 2004; Halvorsen, 2004). This is a typical situation for Scandinavian alpine areas.

It should be noted that an important aspect of climate and hydrology in relation to the biological processes in the upper parts of the Atna watercourse is the amount of snow in spring. Large amounts of snow create snowbeds that may remain in the catchment areas of mountain tributaries through most of the summer, keeping water temperatures low (Tvede, 2004). This has an obvious impact on the various biological processes. Below Lake Atnsjøen, any variation in the characteristics of the river water is dampened by the water reservoir.

Temporal variation

The meteorological time series from the recording stations near Lake Atnsjøen includes precipitation data since 1904, and temperature data since 1864 (Nordli & Grimenes, 2004). Precipitation over these nearly 100 years shows no significant change, whereas there has been a significant increase in annual mean temperature since 1864. The annual frost free period has increased by 13 days per 100 years, mainly due to earlier passing dates in spring. However, the length of the growth season (days with temperatures $\geq 5^{\circ}\text{C}$) only increased up to the 1950s, but has decreased slightly since then. At the climate station at 700 m altitude, the warmest month is July (11.3°C), while the coldest is January (-9.9°C).

Water discharge data are available for the period 1986–1998. The seasonal variation in water discharge normally follows a general pattern. At the outlet of Lake Atnsjøen, there is a minimum weekly mean in early spring (March) around $2\text{ m}^3\text{ s}^{-1}$, and a maximum weekly mean in early June at $29\text{--}38\text{ m}^3\text{ s}^{-1}$ (Tvede, 2004). The variation in annual mean discharge has been restricted over the documented period, with a minimum of $7.5\text{ m}^3\text{ s}^{-1}$ (1991, 1996), and a maximum of $12.4\text{ m}^3\text{ s}^{-1}$ (1987).

In early June 1995, an extreme flooding situation caused severe, although temporal, impacts on physical, chemical, and biological conditions in the Atna watercourse (Tvede, 2004; Halvorsen, 2004; Halvorsen et al., 2004), as well as in the Glomma watershed in general (Eikenæs et al., 2000). It is inter-

esting to note that this situation was brought about by quite normal precipitation. However, a daily rainfall of 25 mm (abundant, but not unusual) was observed on two consecutive days, following several days of rainy weather which had saturated the soil as well as the remaining snow. Thus, an accidental combination of relatively common events caused a nearly catastrophic water flow.

Water chemistry

The Atna watershed is unique in that the human impact is quite insignificant (Tvede & Halvorsen, 2004). Urban and infrastructure development, and intensive agriculture, which normally leads to physical encroachment on the water course and pollution and other chemical modifications of the natural ecosystem, are very restricted in the Atna watershed. Even long distance pollution, i.e. 'acid rain', which has devastated freshwater systems in large parts of southern Norway (Hesthagen et al., 1999), has had little impact in Atna, due to the geographical position of the watershed (Halvorsen, 2004).

The altitudinal gradient of River Atna is reflected in the chemical characteristics of the water. In the mountain area, water pH and dissolved solids are lower than further downstream (Nordli & Grimenes, 2004; Blakar et al., 1997). The concentration of most dissolved solids increases significantly from a locality at 1020 m a.s.l. (Dørålseter) to 430 m a.s.l. (Fossum) (Blakar et al., 1997). Still the water quality at the lowermost reaches of Atna River is very good, with conductivity varying between 12 and $25\text{ }\mu\text{S cm}^{-1}$.

Periphyton

The periphyton of River Atna is typical of riffle communities in cold, nutrient poor rivers with low humic content and low to medium alkalinity (Lindstrøm et al., 2004). The data on periphyton presented in this volume are quite comprehensive. Considering the number of localities sampled, the amount of data available, and the level of detail in the analysis, Atna is one of the best studied alpine–boreal rivers in Scandinavia in terms of periphyton. Moreover, the sampling programme continues to produce even more valuable information (Lindstrøm et al., 2002).

There is substantial variation in the periphyton community along the Atna River, reflecting the gradients in water chemistry and water temperature. Both

species composition and species diversity were closely correlated to altitude, duration of the growth period, total phosphorous, and total organic carbon. While spatial variation is pronounced, the algal community shows good seasonal stability in species composition, and the changes over 12 years of sampling were also small. However, the stability of species diversity contrasts with the extreme variability in periphyton abundance.

The spatial changes appear to reflect quite accurately the changes in environmental factors. The combination of temporal stability and spatial variability in species composition within the watercourse is the main reason that taxonomic periphyton observations have become an important constituent in water quality assessments (Lowe & Pan, 1996). Standard qualitative methods are suitable to reflect periphyton species composition and diversity, but proper taxonomic knowledge is a prerequisite for reliable results. The scarcity of taxonomic expertise on periphyton appears to be the main drawback regarding the usefulness of this parameter in monitoring programmes and in the work to classify waterbodies during the implementation of the WFD (see, e.g., Solheim et al., 2003).

Macroinvertebrates

The investigations of the macro invertebrate fauna of River Atna provides comprehensive data on Plecoptera, Ephemeroptera, Trichoptera, and the dipteran families Chironomidae and Limoniidae (Aagaard et al., 2004). The fauna recorded is typical of running waters of this region, and demonstrates a typical zonation from high altitudes (the alpine zone) to the boreal zone. However, the distribution of functional groups differs from that described in the original River Continuum Concept (Vannote et al., 1980). Atna's sources are in the mountains, where the terrestrial vegetation is very scarce. With no shading, this provides good conditions for aquatic primary production (periphyton), while the supply of terrestrial detritus is restricted. In the source areas of Atna, the grazers dominate the zoobenthos community (Aagaard et al., 2004). This appears to be typical of Scandinavian rivers, which tend to originate in alpine areas.

A second modification of the zoobenthos zonation in Atna compared to Vannote et al.'s (1980) original description, is caused by the presence of a lake in the water course. The export of phyto- and zooplankton

produced in the lake creates a completely different situation for lotic zoobenthos at the lake outlet and some distance downstream (Sandlund, 1982; Haraldstad et al., 1987). This is reflected in the dominance of collectors (i.e. filter feeders) in the insect community at the lake outlet. In many parts of Scandinavia and other areas that were covered by Pleistocene glaciers, water courses are dotted with numerous lakes. The zoobenthos discontinuity associated with lake outlet habitats is therefore a common trait in these rivers.

The present data set on zoobenthos demonstrates some important issues regarding macroinvertebrates in biodiversity monitoring of running waters. There are well established methods for sampling both the insect larvae and nymphs in the water, and the adult flying insects. However, within reasonable sampling effort, a significant proportion of the species present will be missed in an annual sampling programme. With one annual sampling period, 50–60% of the aquatic insect taxa present in the ecosystem will be missing from the samples. By combining the material from 3–4 consecutive years, the number of taxa missing is reduced to approximately 20%. Because monitoring programmes without exception are restricted in available resources, this seems to indicate that standard sampling programmes are not suited for monitoring of species diversity in lotic invertebrate communities. Monitoring of rare species for conservation purposes therefore requires different approaches from the one applied in Atna.

The macroinvertebrates of rivers may, however, be well suited for other types of environmental monitoring. For example, monitoring of pollution (acidification, eutrophication, etc.) may be based on the presence and relative abundance of the common species (Magurran, 1988).

In Lake Atnsjøen, the zoobenthos community is typically oligotrophic. However, in the northern end, the inflowing river brings large amounts of detritus, creating a higher organic content in the sediments. Thus, the zoobenthos community is more eutrophic in this part of the lake (Aagaard et al., 1997). The extreme spring flood in 1995 brought large quantities of inorganic sediments to cover the organic sediments, causing a significant drop in zoobenthos abundance, with a subsequent recovery after 3–4 years (Lindstrøm et al., 2002).

Fish fauna

One parameter that even in the most pristine water courses have been radically altered by man is the distribution and occurrence of fish species (Hesthagen & Sandlund, 1995, 1996; Rask et al., 2000). This appears to be the case in all areas of Europe where man has been active, and is a consequence of the fact that the technique of moving useful fish species to new localities in order to create permanent stores of live food has been known at least since medieval times (Sandlund & Bongard, 2000). This is also the case in the Atna water course (Hesthagen & Sandlund, 2004). Fish are identified in the WFD as one of the groups of organisms that should be used in the classification of water types and their status. The consequence is that the definition of reference condition for most water types will have to adapt to the fact that the fish fauna very rarely is in a pristine condition.

However, the biology of the major fish species is usually very well known, and the necessary taxonomic expertise is common knowledge in many communities. This means that data on the fish community and the status of fish populations are very useful in interpreting the biological condition of the ecosystem (Tammi et al., 2003). Fish are also good indicators of persistent pollutants because of their trophic position and long life span. Finally, collection of data on fish is usually relatively straightforward, with well established methods.

Phytoplankton

Phytoplankton has been a widely used parameter to describe and classify lakes. In particular, algal biomass and productivity measurements are standard variables in most monitoring programmes. Taxonomic analysis has also been commonly included. The phytoplankton observations in Lake Atnsjøen over the period 1990–2000 demonstrate relatively large variations in maximum biomass from year to year, from 125 to 393 mm³ m⁻³ (C.V. = 0.35; Brettum & Halvorsen, 2004). The mean biomass, however, varied less (between 91 and 185 mm³ m⁻³, C.V. = 0.20). Considering species composition, there is a slight change over the years, probably related to the prolonged impacts of the major flooding event in 1995. Otherwise, the phytoplankton of Lake Atnasjøen is fairly typical of deep, high altitude lakes in this region.

Zooplankton

Zooplankton has not been included as one of the major taxonomic groups to be used for classification of water bodies in relation to the WFD. However, good quality data on crustacean zooplankton are available from a vast number of lakes in Europe. Relatively long time series are also available in many cases. Moreover, extensive ecological research over the last more than 50 years constitutes the basis for a good understanding of the dynamics of zooplankton communities and the factors which influence them. It appears reasonable to claim that crustacean zooplankton is the best known and understood group of freshwater organisms in addition to fish. Consequently, to exclude zooplankton from the data used in classifying and monitoring lake ecosystems will usually be unwise.

The zooplankton in Lake Atnsjøen reflects an oligotrophic, high altitude lake with a significant level of fish predation (Halvorsen et al., 2004). The zooplankton community was dominated by rotifers, which constituted approximately 10–15 times the density of crustaceans. Within the crustaceans, copepods were approximately twice as numerous as the cladocerans. The flooding event in 1995 was reflected in the extremely high density of zooplankton that year.

Conclusions

The data on the environment and biota of the Atna watercourse provide an excellent basis for improved understanding and appreciation of the characteristics of an alpine/boreal river system in north-western Europe. The relatively long time series available for several of the data sets facilitates understanding of the natural temporal variation in a pristine river and lake. The fact that data have been collected over an altitudinal gradient from over 1000 down to 350 m a.s.l. adds an important spatial scale. The data reported in this volume might be utilised in further refinement of the definition of the reference condition for this type of water bodies.

Acknowledgements

We would like to thank all contributors to this volume for their good work and positive collaboration. The work for this essay was supported by the Directorate for Nature Management and NINA.

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